THE CONDOR

Volume 62 July-August, 1960 Number 4

JOURNAL OF THE COOPER ORNITHOLOGICAL SOCIETY

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Published bi-monthly at Berkeley, California. Entered as second-class matter at the post office at Berkeley, California, May 15, 1925, under Act of Congress of March 3, 1879. Issued from the office of THE CONDOR, Museum of Vertebrate Zoology, Berkeley 4, California.

MANUSCRIPTS

Send manuscripts for publication to the Editor, ALDEN H. MILLER, Museum of Vertebrate Zoology, Berkeley 4, California, or to one of the Associate Editors, JOHN DAVIS or FRANK A. PITELKA, same address. Refer to suggestions on preparation of manuscripts for THE CONDOR on the back cover of recent issues of the journal.

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Subscription price to non-members, five dollars per volume, payable in advance. Single copies, one dollar each.

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Issued July 29, 1960

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VOLUME 62 JULY-AUGUST, 1960 NUMBER 4

BREEDING BEHAVIOR OF THE BELL VIREO IN SOUTHERN INDIANA

By VAL NOLAN, JR.

In late May of 1958, Bell Vireos (*Vireo bellii*) were discovered nesting at Bloomington, Indiana. Since these birds were some 40 miles southeast of Brazil and 50 miles south of Indianapolis, the previously known outposts at the eastern edge of the breeding range, it seemed desirable to obtain information about them (Brooks, 1942). No intensive investigation was made in that year, but of the three pairs known to have been present, two pairs and their eight young were color-banded and observed for a few minutes a day until mid-July. Three of the banded adults returned in 1959, and the three pairs of 1959 and their ten fledglings were caught. Those not marked in the previous year were banded. A seventh adult, a male that apparently was not mated while under observation, was not captured. Home ranges were visited briefly and irregularly until mid-September, and much of the history of one male is known from the day of his probable arrival until possibly the day he departed. The accumulation of fragments of information on breeding biology and behavior and postnesting activities has prompted this paper, since published data based on banded birds seem to be lacking for the Bell Vireo and are scanty for all vireos.

LOCALITY AND HABITAT

The four fields in which the vireos were found are scattered over a strip about three-quarters of a mile long and one-quarter of a mile wide just north of Bloomington. A previously published account of the topography, land use, and vegetation of an adjoining tract (Nolan, 1955) suffices as a general description of the vireos' area, except as qualified in the present paper. A good deal of such habitat exists around Bloomington, much of it familiar to me for 20 years and to many other naturalists at Indiana University since at least 1883 (McAtee, 1905). So far as I know, the only record of the Bell Vireo from this section of Indiana, other than those reported herein, is my observation of a singing male on September 7, 1953, two miles east of the place where the species now nests. Unfortunately, the home ranges of the birds which Raymond Schneider and I discovered breeding on May 28, 1958, had not actually been visited by me in 1957. However, I had worked regularly in an immediately adjacent tract and had often been within earshot of these fields without ever hearing the familiar song of this species. For these reasons, and because Mumford's (1952) summary of the status of the Bell Vireo in Indiana lists no reports for the state prior to 1943, I believe that the species has only recently established itself at Bloomington.

The habitat of the Bell Vireo was indicated by Ridgway (1873) as being thickets shared with the White-eyed Vireo (*V. griseus*). Bent (1950:254, 259) also records the two vireos occurring together and in his life histories of the Bell Vireo and other brush-dwelling members of the family mentions instances of the Bell Vireo associating closely with its congeners. Hamilton (1958:308, 313), on the other hand, reports that "co-occupancy of the same habitat is almost unknown" among vireos. "[S]ympatric species of *Vireo* show *habitat separation* . . . occurring during the breeding season in different or separate habitats or in different, stratal subdivisions of a habitat . . ."; even the latter type of overlap is avoided by species belonging to the same subgenus. Hamilton's gen-

eralization describes the relations of *bellii* and of the common *griseus* at Bloomington, where the two species keep to separate types of scrub. The essential distinction in habitat seems to lie in the physiognomy of the vegetation, namely, in the amount of medium high, dense cover present. An illustration of the difference is that Blue-gray Gnatcatchers (*Polioptila caerulea*) often nest at Bloomington in the same habitat as do White-eyed Vireos, whereas the Eastern Meadowlark (*Sturnella magna*) is common in two fields where the Bell Vireo is found (compare Sauer, 1952, and Brewer, 1955). Thus the White-eyed Vireo probably never ventures far from the shelter and shade of relatively close-growing stands of 8- to 25-foot trees, whether saplings or mature plants of low, round habit, such as *Crataegus* spp. In the more open, sunny, dry, grassy, and often more extensive areas are Prairie Warblers (*Dendroica discolor*), Yellow-throats (*Geothlypis trichas*) and Yellow-breasted Chats (*Icteria virens*), among the insectivorous birds, and it is in these fields that *bellii* nests; Indigo Buntings (*Passerina cyanea*) and Field Sparrows (*Spizella pusilla*) are also commonly associated species. The only high cover typically consists of a thicket at the base of one or two large trees growing near a sink hole, and/or a row of sassafras (*Sassafras albidum*) or osage-orange (*Maclura pomifera*) along a fence, and perhaps also scattered clumps of one or more scrubby trees from three to 20 feet high. Such fields also contain low tangles of blackberries (*Rubus* spp.) and prairie rose (*Rosa setigera*), in which the Bell Vireo does much of its foraging and sometimes nests. Habitat descriptions by Pitelka and Koestner (1942:97–98), Hensley (1950), and Mumford (1952:226–227) list similar or only slightly less open growth, but Bent's collection of reports indicates that the Bell Vireo will nest in fairly dense scrub. In view of this apparent tolerance of a rather wide range of differences in cover, it may be suggested that an important element in the selection of open habitat at Bloomington is that association with the White-eye is thereby avoided. Some support for this point may be drawn from the fact that pairs of Bell Vireos, during most of the season at least, also avoided intraspecific contacts except those within the family unit. This subject is discussed further in the following section.

LOCALIZATION

"Localization" is used here not to suggest the process by which Bell Vireos form an attachment to a particular place (Scott, 1958), but to introduce data concerning manifestations of that attachment. Also included is the related subject of dispersion over the breeding habitat. Pairs are designated by letters which will be used throughout the paper.

Spacing of pairs.—In no case did two pairs breed in the same field, although, as will be shown, the home ranges of five of the six males studied lay in fields large enough to accommodate more than one range. The closest approach to adjoining occupancy occurred in 1958, when males A and B used fields which, although separate, touched at one corner of each. However, this point was near the top of a long hill, so that the two ranges lay on different slopes and were divided to some extent by this topography as well as by a mowed field lying in the right angle between them. Members of the two pairs were never known to meet, but each male sang once, on different dates, at the common corner; one had travelled about 175 yards from his nest, the other about 130. The maximum distance that could have separated nests built in the two fields would have been about 450 yards; the actual distance between nests was about 250 yards in a straight line across the mowed area. Never as I stood on one home range did I hear both these males singing at the same time.

During the nesting season in 1959, the ranges of the four males lay in a rough north-south line, each in a field bounded on all sides by tracts of wholly unsuitable habitat

for the Bell Vireo. The widths of the unsuitable tracts between the home ranges, that is, the distances by which each male was isolated from the next, were 500, 250, and 400 yards. In late summer Male C from the north and unbanded Male D from the south (the latter identification is assumed) crossed the barriers and settled in Male A's field next to his home range.

The dispersion just described suggests that pairs of Bell Vireos shun contacts with other pairs during nesting. It may be significant that the two males that shifted in late summer had brought off no young. The effect of their moves to points within earshot of another male was perhaps to break what otherwise might have been late summer isolation from members of their species. If there is a breakdown of territory lines at the end of nesting in the Red-eyed Vireo, *Vireo olivaceus* (Southern, 1958:188), this may be a related phenomenon.

Territory.—As already indicated, encounters with other vireos, which might have stimulated defense behavior, were never witnessed. That such behavior is evoked under conditions of population density is shown by Grinnell (1914:189–190), who studied the distribution of the Bell Vireo along a narrow strip of willow association between the Colorado River and the desert. "A singing male occupied each segment of about 200 yards in this belt. . . . Each pair of vireos was closely delimited in its forage beat by that of its neighbor. Each pair in its own area actively resented encroachment by others of its own species."

Home range.—Except for occasional short excursions, pairs confined themselves to a utilized home range of two to three acres, until the young flew readily. The family thereafter occupied an area at least as restricted, but not necessarily identical with that used earlier. After the young disappeared, probably both adults remained on the late summer range of about one acre. I have only one late August record of a female, but this may be because females are silent and hard to discover. Males, on the other hand, could usually be found day after day in the same thicket. Faithfulness to a home range carried over to the following year in the male, and the one female that returned remated with her last year's partner.

The boundaries of the ranges used during breeding became stabilized after the first nest was begun and were probably determined by its location. Sometimes the nest was at the edge of the field in a fence row, but where it was in mid-field it was roughly the geographical center of activity. Occasionally birds were seen as much as 200 yards from the nest; these moves beyond the usual radius of 100 to 125 yards were made along fence rows or strips of cover. Postbreeding home ranges centered around a favored thicket.

The data to support the foregoing summary follow. References are to utilized and not maximum home range (Odum and Kuenzler, 1955). *Pair A, 1958*: This pair used about three acres of a ten-acre field; eight more acres of habitat lay immediately across a little-travelled road. Contact with Pair A was lost in late July when their field, except for the fence rows, was mowed in preparation for a subdivision. *Pair A, 1959*: The adults paired again but moved into the unmolested eight acres just across the road, the habitat nearest their now unsuitable home range of 1958. The two nests of 1959 were 12 yards apart and 180 yards from that of 1958. During nesting there were only two sightings of Pair A outside a two-acre circle with the nest roughly in the center; on both occasions the pair had followed a fence row back to the home range of the preceding year. When fledglings of a second brood could move about, the family went some 100 yards south and seemed to stay very largely within about one acre, much of it covered by a thicket around a sink hole. Just before becoming independent the young enlarged their sphere of activity to include an area of about two acres. Male A could almost

always be found at or near the sink hole until he left. *Pair B, 1958*: This pair probably seldom ventured beyond a line encompassing 2.5 acres in a seven-acre field of uniformly suitable habitat. Two nests were 50 yards apart. I quit visiting the field in late July, when all but about three acres around the nest were cut over. *Pair B, 1959*: Male B returned to the same home range, acquired a new mate, and used approximately two acres of the uncut part of the field. Two nests were 34 yards apart; the first of these was 23 yards from the second nest of 1958. From late July until I last saw them about the middle of August, the adults and young kept to denser cover of fence rows and tree clumps in about one acre of their range. *Pair C, 1959*: These birds were not visited often but during nesting were never seen outside an area of about 2.5 acres around the nest, which was in a corner of the field. The next adjoining acre of their six-acre tract had been eroded or stripped down to bare clay, a sort of barrier which may have confined them somewhat. A nest failed in mid-June, after which I lost the pair, but Male C was found nearly daily in the three weeks before mid-September. He had moved 400 yards from his nesting range, and he rarely left a 15×55-yard strip (about 0.17 acres) of fence row and blackberries. *Male D, 1959*: Male D occupied a field containing about six or seven acres of habitat. His home range covered an area of 2.5 acres, but he made more frequent sorties from it than did the other males, possibly because he had no mate. Some days he could not be found, and in late June he disappeared; an unbanded male that turned up at the end of July 350 yards north of the range of this male was thought to be Male D. During molt he moved again, another 250 yards north across the range of Pair A, where he remained until last seen in late August.

[In 1960 all six banded adults of the preceding year returned to their home ranges, except Male B. Pair A remated, as did Pair C, but the latter pair disappeared after about a week. Female B was present for only two or three days. There were also an unbanded pair and three, unbanded, unmated males.]

Other authors have found single pairs of *bellii* using a three-acre tract (Pitelka and Koestner, 1942:97) and having a home range of 3.1 acres (Hensley, 1950), but in the latter case it is impossible to tell whether more extensive habitat was available and whether other pairs were present. Territory size of *olivaceus* has been reported as averaging 1.4 and 2.1 acres (Lawrence, 1953:51–52) and 1.2 acres (Southern, 1958:109). Brewer (1955) describes a home range of 0.33 acres for one pair of *griseus*, but my own unpublished observations of color-banded birds of that species suggest a larger area.

ARRIVAL AND PAIR FORMATION

Male A first sang in 1959 on May 6, after several warm days and nights, and since male Bell Vireos are in full song even while migrating through Central America (Dickey and van Rossem, 1938) it is probable that Male A had just arrived. Loud songs at a rate of 15 per minute were uttered from middle heights in 10- and 15-foot trees. Most movement was over about two acres immediately south of what was to become the home range; once he covered 200 yards and sang from that future center of activity. Frequent song, uttered from the clumps of trees, continued next day. At 6:30 a.m. (all times herein are central standard) on May 8 an unbanded bird, assumed to have been a female, was present. I became aware of this when Male A quit singing and flew about 20 yards on stiff, horizontal, scarcely beating wings. Suddenly the female flew out of blackberries near him and for 10 or 15 seconds there ensued a rapid twisting pursuit, the male from one to four feet behind the female and both ranging in height from one to eight feet. The chase was interrupted when the two landed in a bush and pecked or pulled with their bills at each other for two seconds before darting another 30 yards out of sight in

the brush. Male A then flew to a tree near me and for 1.5 minutes sang every few seconds until the female suddenly reappeared, in the berries ten yards from him. She was immediately pursued as before, again with the interruption for pecking at each other. At the end of the flight the birds lit five feet apart in a bush, where both flicked their wings and flirted their tails laterally in rapid movements closely resembling those made in dew-bathing. (These wing and tail movements occur frequently between mated Bell Vireos and are often given when the two are close together, continuing at least until young leave the nest.) In a few seconds one bird spread its tail slightly and hopped toward the other, which retreated; both then moved into the brush and were out of sight for 20 minutes.

When rediscovered the vireos were some 60 yards beyond, and their behavior seemed to have entered a second stage. The female now moved slowly through the thickets, about 20 yards at a time, the male following, landing some ten yards from her, singing once or twice, and then in silence rapidly flicking wings and tail until the next move. In ten minutes or more, during which 250 yards were covered, there was only one variation in this: then the male approached to within two feet of the female, she raised and spread her tail, and he hopped way. Two hours later the birds were back where I had first seen them, still moving along together in the manner just described.

During the next two days Male A sang about 15 times per minute from 10- to 15-foot perches. This constant singing and my inability to find the unbanded female made it clear that she had gone. On May 17, the banded mate of the previous year was present. Nest building had already begun on this date, and that fact and the scarcity of songs by Male A from May 11 through May 17 suggests that the pair had been formed on May 11 or very shortly thereafter. Red-eyed Vireos fall silent temporarily immediately after pair formation (Lawrence, 1953:52).

One other episode, on June 6, between unmated Male D and a second bird so closely parallels the observations just described that it seems probable that it involved courtship and not agonistic behavior. There was the same close rapid pursuit (covering 40 yards, reaching 25 feet in height, with faint notes audible from a few yards distance), the same wing and tail quivering as the two birds perched, the same temporary disappearance of the newcomer during which the male sang loudly, and finally a series of short flights together through the brush. In this case, too, no pair was formed, for the second bird left after I had watched for about 15 minutes. For the next 20 minutes Male D sang steadily from the highest perches on and around his usual range, most of them 30 feet or more high; about two minutes were spent on each perch. On subsequent days he sang the loud, regular song that seems especially characteristic of unmated males. He never scolded me as mated males do when one is near the nest.

It is possible that one or both of the foregoing episodes involved two males, but because of similarity with the courtship of other vireos I think this is not likely. I have seen following and wing-quivering in the pair formation of color-banded White-eyed Vireos known to be male and female, and Lawrence (1953:53) reports comparable behavior in Red-eyed Vireos. Lawrence also describes a first meeting between male and female Red-eyed Vireos characterized by a fast twisting pursuit to the ground, and Southern (1958:114) records much the same thing in the courtship of Red-eyed Vireos, as does Lewis (1921:28) in that of Philadelphia Vireos (*Vireo philadelphicus*).

Grinnell, Dixon, and Linsdale (1930:364) write of two Bell Vireos on April 23: "One, probably the male, was singing and keeping within one meter of the other, both moving through the low branches, feeding. The singing bird kept its tail spread and frequently gave it a twitch, spreading the feathers still more. Also at intervals the tail was pushed downward to a nearly vertical position."

NEST BUILDING

The interval between pair formation and building by Pair A, which had been mated before, can have been no greater than five days. Five to six days is the length of the same period in the Red-eyed Vireo (Lawrence, 1953:54), whereas about two months elapse between the arrival of males and nest building in the tropical Yellow-green Vireo, *Vireo flavoviridis* (Skutch, 1960:14, 25).

Twice when predators destroyed nests, one containing eggs and the other young, replacement nests were found immediately; building had evidently begun no later than the day after the first nests failed. Nice (1929:16) and Pitelka and Koestner (1942: 98–99) report equally prompt renesting.

There was no systematic observation of building, but both sexes were seen with material, the male sometimes singing with it in his bill. Once Male B was noted carrying plant fibers at a time when the first nest had probably not yet been begun. During building the male usually accompanied the female very closely as she ranged as much as 85 yards from the nest. In my own brief experiences he sang little, for example, on one occasion 15 times in 15 minutes, but Mrs. Nice (1929:16–17) and Hensley (1950) found males very vocal at this stage.

Duration of building is known relatively precisely only for the two replacement nests, which were constructed in a maximum of four days each. The only first nest found in the building stage must have required considerably more time, for insertion of the thin, grassy lining alone took three days. Four to five days is the period reported by Mrs. Nice (1929:16), Pitelka and Koestner (1942:99), and Hensley (1950). Calculation of duration of building and of the interval before laying is complicated because the birds often come to the nest even after it is functionally complete and at times add material to it. Male B once affixed a spider's egg case after Female B had laid her first egg. This habit of prolonged building is found in *Vireo philadelphicus* (Lewis, 1921:31), and in *Vireo olivaceus* it persists until after the eggs hatch (Lawrence, 1953:56; Southern, 1958:126). Skutch (1960:17) saw one instance of nest reinforcement by an incubating Yellow-green Vireo.

NEST TREES AND NESTS

Eight nests were built in the course of the study, two in white elms (*Ulmus americana*), two in sassafras (*Sassafras albidum*), two in blackberries (*Rubus* sp.), one in sugar maple (*Acer saccharum*), and one in osage-orange (*Maclura pomifera*). All trees but the last ranged in height between four and seven feet; the osage-orange was 12 feet high. The blackberries grew among patches along fence rows, whereas the trees either stood alone or were at the edges of little clumps of saplings measuring six feet or so across. Ground and field cover around the nest trees and bushes consisted of grasses such as *Poa compressa* and *P. pratensis*, *Triodia flava*, and *Aristida* sp. and such forbs as *Daucus carota*, *Asclepias* sp., *Plantago* sp., *Solidago* sp., *Erigeron* sp., *Achillaea millefolium*, *Cirsium* spp., and *Chrysanthemum leucanthemum*. Some of these, as well as blackberries, reached as high as the branches in which the nests were placed.

All eight nests were suspended from and fixed tightly in lateral forks ranging in angle from 45° to 85°, and one was fastened also to a second lateral twig which thus provided support on a third side. The minimum height was 23 inches, the maximum 34, and the average about 28. Except for the blackberry nests, all were placed between six inches and one foot from the end of a branch at a point where it was nearly horizontal. The osage-orange nest was five feet out from the trunk; the others were between one and two feet out. Supporting twigs were from about two to five millimeters in diameter, and terminal leaf clusters of the nest limb and sometimes of limbs above it provided

shade and some concealment. Nests built in blackberry bushes were in lateral forks of horizontal or slightly diagonal canes growing from a main leader; there were numerous new leafy shoots nearby.

Most nests were slightly oval-shaped cups, with the long axis of the oval bisecting the angle of the suspending fork. Rims were slightly constricted, and the apertures of nests in acutely angled forks were wedged-shaped segments of circles. Except for one dimension, depth, it is unnecessary to record in detail the measurements of four nests, since they closely approximate those reported by Mumford (1952) for seven Indiana nests. Depths of the cups of four nests were 47, 46, 45, and 44 mm., averaging 45.5 mm.; Mumford's maximum inner depth was 38 mm., and his average was 34 mm. Outside depth measurements of the same four nests were, respectively, 58, 68, 55, and 64 mm., averaging 61 mm. Average outside diameters were 68×60 mm., and average inside diameters were 51×44 mm. Weights, in grams, of dry nests were 5.6, 5.5, 5.2, and 5.0.

Nests have two parts, a relatively thick outer cup and a thin lining. Externally they are a general smoke gray (Palmer and Reilly, 1956), deriving their color from the weathered bast fibers and leaf fragments which are the major components of the cup. The lining is composed of three- to five-inch culms and axes of inflorescences of grasses (*Aristida* sp. and others) and is between buffy brown and dark smoke gray in color. The many cottony, 3- to 12-inch fibers (most of them probably from *Asclepias* sp.) of the cup are somewhat matted and stiffened by rain and dew into a tight, hard, resilient structure. Spider webs seem to form an important ingredient only near the rim, sometimes lending a whitish color to that part, from which they may spill down one-half inch or so on both inside and outside. Egg cases of spiders are also used in small quantities on the outside of the cup. Pieces of leaves no larger than about one inch square are a conspicuous element in the nest, especially toward the bottom, their proportion varying from a few fragments on the outside to a sometimes almost solid pad added just before the grassy lining. One nest had several bits of newsprint, another some papery outer bark probably from a young sumac (*Rhus* sp.), while a more interesting leaf substitute was 50 or so pieces of the thin bright orange outer bark of an osage-orange root exposed 25 yards from a nest. It is probable, judging from the texture of the cup, that the fibers are placed in random directions across the nest rim after a shell has been formed and are pressed into position by the body and limbs; loose ends presumably are fastened in place by the bill. The texture of the grassy lining indicates a similar random placement; incomplete nests in the lining stage sometimes have many pieces of grass in a loose mass in the cavity. In one nest the total weight of the long fibers was 2.3 gm., of the leaves and osage-orange root bark 2.1 gm., and of the grass lining 0.6 gm.

EGG LAYING AND EGGS

The period between completion of the nest and the laying of egg 1 was, in two first nests of the year, one and two days. In two replacement nests there were a one-day interval and no interval. Mrs. Nice (1929:16) noted a time lapse of one or two days until laying, Pitelka and Koestner (1942:99) none or one day, and Hensley (1950) none. On most occasions when I have seen the pair at this stage they have been together, the male relatively silent, although twice the male was singing at or near the nest.

Female A's first egg in 1959 was laid on May 22, which was 16 days after the arrival of Male A and about 11 days after Pair A was formed. Of the other seven nests studied, dates for the laying of egg 1 are known or can be calculated for four nests discovered before or in the course of laying. These dates are, for two first nests, May 25 and May 26, and for two replacement nests, June 10 and June 16 or 17. In two nests found with

young, the beginning of laying can be fixed within one or two days as May 16 and July 1, the latter involving a second brood.

Clutch size in seven nests was four, but for three nests this figure is based on the fact that they contained that number of eggs or young when found; a fifth egg or nestling might already have disappeared. The eighth nest was the only one parasitized by the Brown-headed Cowbird (*Molothrus ater*), and it held two cowbird eggs; the three vireo eggs cannot safely be assumed to have been a complete clutch.

Eggs were marked in nests discovered during the early stages of laying. It was found that the eggs were laid on consecutive days. The hour of laying was probably at or just after dawn, because the egg was invariably deposited after my visit in the late evening and before my next visit between 5:30 and 6:00 a.m. the following day. Once a male was found perched beside the nest at 5:15 a.m., with the female on a newly laid egg, her third. Southern (1958:121) and Lewis (1921:32–33) record similar hours of laying for other vireos, but Mrs. Lawrence (1953:57) noted exceptions in a pair of Red-eyed Vireos.

Measurements of Female A's first clutch in 1959, in the order in which the set was laid, are 17.7×13.2, 17.9×13.4, 18.1×13.4, and 18.3×13.5 mm. Female B's two sets in 1959 were measured in the order laid, except that egg 2 in the first set disappeared before it could be measured. Also, the second nest when discovered held only a cowbird egg, so that the first vireo egg found may have been in fact the second vireo egg laid. With dashes to indicate these gaps, egg sizes were: 17.7×13.0, —, 17.0×12.8, 16.9×12.8 mm. in the first set; and —?, 17.1×13.0, 18.0×13.0, 18.4×13.0 mm. in the second set.

INCUBATION AND HATCHING

Roles of the sexes.—Both male and female Bell Vireos sit on the eggs, and the species is uniformly placed on the list of those vireos in which the male incubates. However, in the Bell Vireo, as in all (Bailey, 1952:134) or most (Skutch, 1957:77–78) passerines, males have no incubation patch. This was true, at least, of Males A, B, and C, all of which were examined during the stage of feeding nestlings. Male A was examined in both 1958 and 1959. Lacking a patch, males cannot warm the eggs efficiently (Kendeigh, 1952:168, 274–278; Bailey, 1952:128; Skutch, 1957:77); and it seems probable that their attentive periods at the nest serve other functions than incubation in the strict sense, although Skutch (1957:78) suggests that this is not necessarily true. Among these functions may be included keeping track of the general situation and requirements of the family, such as discovering the presence of nestlings as soon as they hatch (Skutch, 1953; 1960:18–20), and standing guard. Mrs. Nice (1929:15) saw a male Bell Vireo drive away a Brown Thrasher (*Toxostoma rufum*), and Mumford (1952:230) observed the repulsing of a female cowbird; but in neither of these instances had the male been covering the eggs at the moment of intrusion. Such guarding is not confined to the females' periods of inattentiveness, for males often sing in the nest tree (Nice, 1929:15), and by the time the eggs have hatched there is usually a great patch of droppings on the leaves below a favorite perch. The male Solitary Vireo (*Vireo solitarius*) is a silent watcher near his nest (Bent, 1950:311).

Conservation of heat supplied the eggs by the female, shelter from direct exposure to sun and rain, and reduction of losses from wind and storms (as in an instance described by Southern, 1958:124, for the Red-eyed Vireo) are other possible or probable results of the male's covering the eggs. In evaluating the relative importance of the possibilities suggested, it may be noted that, unlike the female, the male Bell Vireo often leaves the nest to sing at and scold the observer the minute his approach is noticed.

Thus, I seldom saw a male sitting on the eggs but only detected him when he was slipping away from the nest. Bennett (1917:288–289) describes a "characteristic" incubation habit of "sitting absolutely motionless at the edge of the nest . . . at more or less regular intervals," sometimes of 10 or 20 minutes. He ascribes this behavior to both sexes, but he worked with unmarked birds and I wonder if the habit he saw was not primarily the male's.

If it is true that the male does not warm the eggs, data on the relative attentiveness of the sexes are of special interest. My observations are scanty. Nests were inspected 59 times from the day the last egg was laid through the day on which hatching began, and females were found sitting 35 times (59 per cent) while males were present 22 times (37 per cent). These percentages compare closely with those determined by Hensley (1950) by prolonged observation of one pair; a female spent 56 per cent of 206 minutes on a nest and her mate spent 43 per cent. While this degree of female attentiveness is below that of most passerine species in which the male does not incubate (Nice, 1943: 221–222, 227), the comparison of greatest interest is with figures for other vireos in which the females alone cover the eggs. In the Red-eyed Vireo, Southern (1958:128) reports extremes of attentiveness for eight females as being 52 and 82 per cent; the range for five females watched by Mrs. Lawrence (1953:60) was between 71 and 83 per cent. Four female Yellow-green Vireos incubated for periods varying from 62 to 77 per cent of the observation time (Skutch, 1960:16, 27), and a Gray-headed Greenlet (*Hylophilus decurtatus*) spent 52 per cent of the time on her eggs (*ibid.*:31, 34).

Returning to the Bell Vireo, my records of the distribution throughout the day of the time spent on the nest by the male and female alter the picture presented by mere percentages of attentiveness. In 37 nest inspections before 9 a.m., I found the male present 21 times, the female 14. On 22 inspections after 9 a.m., the male was at the nest once, the female 21 times. Thus the ratio of attentiveness of the male and the female in the early morning was 3:2, and 95.5 per cent of the male's time at the nest and 40 per cent of the female's time were attributable to the early hours of the day. There was no noticeable change in proportion or hourly distribution correlated with time advance of incubation. I would conclude that these facts, incomplete though they are, indicate the need for much further investigation of incubation patterns and egg temperatures before we shall understand the roles of the sexes in those vireos in which both male and female sit on the nest.

A full sequence of nest relief was watched only once. The male approached the nest apparently with caution but sang a few yards from it, and he sang again ten yards from it when relieved by the female 15 minutes later. Possibly the songs were directed at me, but since the male Bell Vireo, like many other vireos, sings on the nest (Bennett, 1917:289; Nice, 1929:15), this was not necessarily true.

Beginning of incubation and sequence of hatching.—In three of five nests found on or before the day the first eggs were laid, females were seen sitting before the clutch was complete. That some warming occurred at these times is indicated by the sequences of hatching: In four marked or partly marked clutches, the last egg laid was the last to hatch, in two the third egg laid was next-to-last to hatch, and in one the first egg laid was the first to be pipped. In no instance was an egg known to hatch in a sequence differing from that of laying.

A measure of the amount of early incubation is to be found in the times elapsing between the hatching of eggs in a clutch. The most precise figure available is for one interval between the hatching of eggs 3 and 4; it was 26 ± 2 hours. Another such interval was more than ten hours. The period between hatching of the first and next to last eggs was known in one instance (unmarked eggs) to be about seven hours, and in another

instance it could be fairly guessed to be at least 12 hours. At the latter nest a newly hatched bird from egg 3 at 6 a.m. weighed 1 gm. while its largest nest mate had already attained 1.8 gm., which is only 0.2 gm. less than a nestling has been found to weigh at 25 hours of age. Variable though weights are, the difference of 0.8 gm. shortly after dawn suggests that the largest bird hatched the preceding day. If so, then the interval between the first and last hatchings in this set was 36 hours or more, and hatching extended over three days. Lewis (1921:40–41) reports a similar instance for a set of eggs of the Philadelphia Vireo.

All the foregoing data are from situations in which there must have been substantial incubation before the clutch was complete, in one instance beginning probably with the laying of egg 2. The opposite is indicated for the nest in which only three eggs were found, namely, the nest parasitized by the cowbird. I removed the two cowbird eggs when the vireo's laying was complete, and on four visits to the nest during laying never found an adult on the nest. The first of the three vireo eggs failed to develop; the last two laid pipped nearly simultaneously and two nestlings of the same size were present on my next visit. Incubation therefore began probably shortly, if at all, before the last egg was laid, a fact which may be related to molestation by the cowbird or to the possibility that the complete clutch consisted of three rather than the usual four eggs. Mrs. Lawrence (1953:59) reports beginning of incubation in Red-eyed Vireos after the laying of egg 3, whether the full set consists of three or four eggs.

The variability in the start of incubation in the Bell Vireo is reflected in the reports of others: Mrs. Nice (1929:13) found it beginning with egg 3, Pitelka and Koestner (1942:99) with egg 1, and Hensley (1950) with egg 2. Southern (1958:122) noted similar irregularity in *Vireo olivaceus*.

Duration of incubation and hour of hatching.—On the assumption that eggs were laid between 5 and 6 a.m., the period of incubation for three marked fourth eggs was 13 days, 16 ± 10 hours; 13 days, 20 ± 6 hours; and 14 days, 2 ± 2 hours. In an unmarked set the last egg to hatch did so 13 days, 18 ± 6 hours after egg 4 was laid. In a nest in which the hatching time of egg 4 is unknown, egg 3 hatched exactly 14 days after it was laid. All other investigations report a like incubation period of 14 days.

Fine cracks and one or more tiny convex irregularities become visible toward the large end of the egg about 24 hours before the egg hatches. The bumps may enlarge as time passes, but often no further change is noticeable until a true hole is cut. In one instance the hole appeared about two hours before the two shell halves were forced apart. Southern (1958:127) records five hours and ten minutes from the first sign of hatching to the emergence of a young *olivaceus*.

The hour of hatching is known fairly closely for only five eggs; three hatched between 4:30 a.m. and 8 a.m., one at 12 noon, and one between 2 p.m. and 5 p.m. Three more hatched between dusk and my inspection next morning at 5 or 6 a.m. Southern (1958:127) learned that the majority of eggs of the Red-eyed Vireo hatch during midmorning.

NESTLING PERIOD

Parental behavior.—Disposition of the eggshell was seen once. When the female flushed from a nest at 5 a.m., it was found to contain newly hatched young and half a shell. The female returned to brood but quickly left when the male brought food. He then took the shell and flew out of sight.

The foregoing incident shows that males begin to feed the young promptly. Other data are sufficient only to reveal that both adults participate in nestling care, that brooding by the female is probably more frequent than covering by the male, and that after

the oldest nestlings are about seven days old the parents normally spend little time at the nest during the day. Mrs. Nice's (1929:17) data support these general impressions, as do Hensley's (1950).

Males are quick to scold at a person approaching the nest; I found their songs less frequent after hatching. Females too sometimes scold intruders, but more frequently they simply disappear into the brush.

FLEDGING

The hour of departure from the nest was usually before the middle of the morning. One bird is known to have left between 6:30 and 9:15 a.m., one before 7:45, two before 11, and one before 8:45. One brood left sometime after 8:30 a.m. There was no known case of afternoon nest-leaving, but for several young that possibility cannot be excluded.

In three of the five nests producing fledglings, the members of the brood left on the same day. In a fourth, one bird left on June 17, two on June 18, and the last on June 19. In the fifth nest, there was a similar three-day fledging period.

Ages of young of two broods in which all nestlings of the brood left the nest on the same day can be determined to the nearest 12 hours (half-day); two left at age 10.5 days, one at 11.5 days, and three at 12 days. In the two nests in which fledging was prolonged over three days, the assumption is made that departure took place in the same order as hatching, that is, the oldest bird first and the youngest last; two young left at age 10.5 days, four at 11 days, and two at 11.5 days. Two of those leaving at age 10.5 days belonged to the same two-young brood; all others were in broods of four nestlings. The maximum error in these calculations of age is about 12 hours; if error is present, it affects only the figures within the extremes of 10.5 and 12 days without altering the extremes themselves.

Pitelka and Koestner (1942:99–100) found that the two nestlings which hatched in a nest parasitized by a cowbird fledged on the same day, after 11 days of nestling life. Hensley (1950) reports a nestling life of 12 days for four young, but he does not say whether they left on the same day and he seems not to have established the dates of hatching.

DEVELOPMENT OF NESTLINGS

Weights and measurements.—At hatching one nestling weighed 1 gm.; its two nest mates, the larger of which was probably 12 hours or more old, weighed 1.8 gm. and 1.2 gm.; one egg was still unhatched. Table 1 presents weights and measurements of nestlings at other ages.

Table 1

Weights and Measurements of Nestling Bell Vireos

	About 12 hours	25 hours[1]	About 60 hours[1]	144–168 hours[2]	144–168 hours[2]	144–168 hours[2]	144–168 hours[2]
Weight	1.8 gm.	2.0 gm.	3.3 gm.	6.8 gm.	8.0 gm.	8.2 gm.	8.3 gm.
Culmen, from base	3.6 mm.	5.6 mm.	6.8 mm.	7.8 mm.	8.3 mm.	8.1 mm.	8.4 mm
Gape	7.3	8.7	10.0	11.0	11.0	11.4	11.0
Tarsus	6.5	7.6	10.4	16.5	17.0	18.4	18.0
Hand	6.0	7.0	10.5				
Forearm	5.2	5.8	8.0				
Folded wing				23.1	27.0	29.7	27.5
Closed eye	5×5.5	5×6	6×6.5				
Eye slit	2.0	3.2	3.3				
Open eye				3×1.7	3×2	3×3	3×2

[1] Youngest and oldest members of brood of four.
[2] Members of same brood.

Plumage.—Young are naked at hatching. The body color is between flesh and rufous (Palmer and Reilly, 1956) except where folds of the straw yellow skin obscure the underlying colors. The bill and tarsi are buffy yellow, the latter with flesh undertones; the closed eye is dark gray; the gape was not compared with a color chart but is a shade of yellow. Twenty-four hours later darkening humeral and spinal tracts are becoming visible and hair-like projections about 0.4 and 0.1 mm. long, respectively, have emerged at the locations of the papillae of the primaries and rectrices. My notes fail to record that the alar tracts are marked by darkening papillae, but I think that they are. At age 60 hours the capital, spinal, and humeral tracts appear as rows of dark dots beneath the skin; the femoral and ventral pterylae are visible as light-colored dots; the crural tract papillae show, but my notes neglect to state their color. The quills of the remiges project 1 to 2 mm. through the skin, and the alar tracts are dark.

There is a gap in my notes until age six to seven days when quills have emerged in all pterylae. Feathers are appearing at the tips of the sheaths of rectrices and remiges and in spinal and ventral tracts. The ventral feathers project about 1mm.; the primary feathers extend about 5 mm. beyond the distal ends of the sheaths, which measure as much as 14 mm.; the sheaths of the rectrices are 2.5 mm. at the maximum.

After seven days of age there is a marked change in appearance as feathers rapidly emerge on all tracts; the dorsal apteria appear to be covered as the young sit in the nest. The young birds cannot be handled beyond this age without risk of disrupting nest life. At the time they leave the nest they are typical tailless passerine fledglings. I took no detailed notes on appearance at this stage but saw nothing at variance with Forbush's (1929:195) general description.

Behavior.—Newly hatched birds attempt to right themselves, using the head and moving the limbs in this effort. At 12 hours the head is lifted for about four seconds in order to gape; this response could not be elicited by squeaking or by probing the body or tapping the surface on which it rested. At 24 hours pulling of the muscles of the eyelid can be seen; my notes do not show when the eye opens.

Banding is best accomplished when the young are six to seven days old. The young now sit with bills at a 45° angle. Crouching in the nest was once noted when I appeared, or perhaps when I or a parent bird was heard, and removal of a nestling from the nest invariably causes the brood to give loud nasal cries somewhat resembling the sounds made by steady blowing on small toy tin horns. This greatly excites the adults, whose scolding notes, however, elicit no evident responses in the young. Like other nestling vireos, young Bell Vireos hold tight to the lining of the nest with their feet when one tries to handle them. However, once out of the nest, birds gape, eyes open, apparently orienting toward their handler; sometimes the eyes soon close as though the effort to keep them open is too great. At six days slight and steady progress over the ground is accomplished by kicking, the wings being extended at times, evidently both as props and for balance. At seven days movement on the ground is better coordinated. At this age the bird can sit upright with its tarsi flat along the surface, and simultaneous kicks of both legs project it forward in jumps of two or three inches.

Although an attempt to remove a nestling from a nest of young aged eight to nine days will cause some of the brood to jump out, they can be returned and induced to remain for two days or more if the cupped hand is held over the nest briefly. Birds at this age are still poorly equipped for survival in the open; their movement through grass is ineffective. They cannot escape from an ordinary glass jar six inches deep and about 3½ inches in diameter with an open top 2½ inches across. Nasal crying continues, and once two young in darkness between my cupped hands uttered faint *peeps* reminiscent of chicks.

Calling from the nest in a long series of loud single nasal cries was heard from a nestling about 10.5 days old left alone by its mates and possibly temporarily neglected by its parents. The calls continued despite the scolding addressed to me by the adults.

At the age of nest-leaving the fledgling moves through brushy field cover perhaps as much as 30 yards in several hours, but the extent to which this is accomplished by flight was not learned. A young Red-eyed Vireo aged 10 or 11 days could travel 12 feet through the air (Lawrence, 1953:68), and a 13-day old fledgling Philadelphia Vireo covered 60 feet in a descending flight (Lewis, 1921:192). A Yellow-green Vireo flew at least six feet just after leaving the nest, and a Gray-headed Greenlet managed 25 feet in a downward course (Skutch, 1960:25, 33).

SECOND BROODS

Mumford and I on August 21, 1958, found four unbanded young about 40 to 45 days old, and although they could not have been produced by pairs A or B, the date suggested that they were a second brood. There are also items in my notes for July, 1958, on Pair A that in retrospect lead me to think that a second brood was attempted before the habitat was destroyed. In 1959, on July 26, Schneider and I discovered Pair A near a nest of four eight-day old young 12 yards from that pair's first nest. To clinch the question of ownership we put up a mist net and caught Pair A at the nest, holding them until it was clear that no other adults were in attendance. Although statements are numerous that various vireos, including the Bell Vireo (Scott, 1888:33), may or do have more than one brood, I find no other verification by banding. Morse (in Bent, 1950:256), however, described a double nest, one with young and the other with eggs, presumably attended by the same pair of Bell Vireos; and Solitary Vireos have been seen building a nest while fledgling young begged for food (McLaughlin, in Bent, 1950:308).

The second brood of Pair A was discovered too late to answer a number of interesting questions, for example, whether the male sits on the eggs or leaves the nest unguarded in order to be able to feed the earlier fledglings. Young of the first brood were 49 days old and had left the home range when the second nest was discovered. A timetable for Pair A shows the first brood leaving the nest in the period from June 17 to 19 (they remained within about 75 yards of it for several weeks) and the second brood leaving on July 28. Assuming that the various stages of the second nesting were of normal length, egg 1 of that brood must have been laid on or about July 1 and nest construction begun on about June 26, about seven days after the last fledgling left the earlier nest. Care of the young of the second brood occupied Pair A, or at least Male A, until his molt appeared to be virtually complete, and the last juveniles were found on the home range on September 2, at age 46 or 47 days.

DEVELOPMENT OF FLEDGLINGS

My appearance on the home ranges evoked such excitement in the parents, especially the males, during the two weeks after the young left nests that I learned nothing about the fledglings except that they apparently dispersed within a radius of about 30 to 60 yards from the nest and there remained hidden in thickets while both parents fed them. The male sang daily, usually in little bursts of three or four songs a minute, followed by irregular intervals of silence. Hensley (1950) found young 30 feet from the nest the day after leaving and 300 feet from it five days later.

At age 25 days a juvenile uttered high, tinny, adult-like notes when fed; it was four feet from the ground. Three days later, ten feet high in a dense growth and 35 yards from its nest, it called a series of one and two nasal notes, not so vigorous as an adult's; these seemed to be location calls to maintain contact with the parent. At this age the bill was

still slightly thickened in the rictal region but the remiges, rectrices, and feathers of the back resembled those of an adult. The head and neck were scrawny and ragged, with bare skin visible. The inverted V of the incoming feathers of the ventral tract extended half-way back on the belly and appeared light buffy yellow in contrast with the grayish white of the juvenal plumage being replaced.

Two broods were observed when they were 35 days old. By this time only the head appeared to be molting, although close examination would have revealed body molt. Traces of raggedness on the head were not noticed beyond age 41 days, after which it would be difficult to age a bird on the basis of its appearance in the field.

By age 35 days the young had become very gregarious, trooping about freely and seldom separating by more than 20 yards. Often the entire brood followed the first to fly and perched in the same bush, where individuals might be as close as a foot or two apart. Occasionally, two or more birds engaged in a short chase. A nasal call indistinguishable from that of an adult seemed to serve both to signal location to siblings and to scold the human intruder. Association with fellows was not constant, however, for a 37-day old bird was found approximately 100 yards from the others. At that distance it sang steadily for about five minutes, giving long, rambling sub-songs.

In addition to the vocalizations already described, I heard single adult-like songs, some *sotto voce*, by unbanded young in a group of four on August 21, 1958. Mumford and I collected one of these, a female; the ragged plumage of her head indicated an age of about 40 to 45 days, as did the behavior and extreme gregariousness of her presumable siblings. Young Red-eyed Vireos and Warbling Vireos (*Vireo gilvus*) sing adult-like songs in late summer (Sutton, 1949:16, 26).

The age at which a bird was last seen being fed was about 30 days, but some feeding almost surely occurs thereafter, probably for about ten more days. A 41-day old juvenile followed one to three feet behind the male parent and fluttered its slightly extended wings as it begged, but I lost sight of the birds after a minute or two. At this age the young could feed themselves without help, even executing such complex maneuvers as swooping to recover dropped food before it touched the ground. Mrs. Lawrence (1953: 68) saw 35-day old Red-eyed Vireos being fed, but 42-day old young were disregarded when they begged. Tyler (in Bent, 1950:338) noted a similar long period of dependence in the same species. Sutton (1949:27) refers to full-grown Warbling Vireo broods begging from the adults.

As to whether the brood splits and leaves the home range separately or moves off together, there is evidence pointing to both alternatives: A careful search of the field of Pair A when the second brood was about 47 days old turned up only two young, which were not associating. On the other hand, the four 40- to 45-day old birds found by Mumford and me remained very close together for at least two days and were in a field in which they had not been seen before. Their parents' home range was unknown, but the nearest possible field, that which was used by Pair C in 1959, was 350 yards away. Sutton (1949:15) believes that broods of Yellow-throated Vireos (*Vireo flavifrons*) stay together until they go south, but this opinion is not based on marked birds. Mrs. Lawrence (1953:68, 70, 74), who made a day-by-day study of a family of Red-eyed Vireos, apparently unbanded, reports that the brood stayed on the adults' home range until 42 days old, when the entire family started to migrate. Southern (1958:188) disagrees with Mrs. Lawrence and states that broods split up shortly after leaving the nest, but he may not have given sufficient weight to the possibility that they reassemble, as do Bell Vireos, when they achieve the stage of easy flight.

In the 40- to 45-day-old unbanded female collected on August 21, 1958, close examination revealed a complete body molt still in progress. This bird weighed 10.4 gm. at

6 a.m. and had an incompletely ossified skull and an ovary about 1×1.5 mm. in size; there was no fat. Without a chart for comparison, the gape was judged to be flesh color and the tarsi bluish gray. The arc of the wing measured 56 mm., the tail 46 mm.

ADULTS IN LATE SUMMER

Behavior.—Several important aspects of late summer behavior have been mentioned earlier in other contexts, namely, that birds may be tending young until the end of August, throughout most of the molt; that home range shrinks in size and may shift and that males spend much time in a single thicket; and that only once has a female been seen. Singing continues in the male, usually diminished to brief series of five to ten songs at a time but not terminated during molt. One male seemed to skulk after molt, singing only occasionally from a berry thicket where he was almost impossible to find, but others at the end of August sang at heights of 35 to 40 feet from conspicuous perches, as males do at times during breeding. Bennett (1917:285) speaks of the species' "retiring habits in late summer."

Molt.—Both males A and B showed signs of molt before their mates did. The date of onset can be roughly fixed because the members of Pair B, when banded on July 2, 1958, were not molting, but Male B on July 20, 1959, and Male A on July 26, 1959, were molting heavily. Male B, watched on July 20, had lost many feathers on the anterior half of the body and some skin showed about the ear; when he preened an extended wing a short inner primary was visible and some of the coverts were missing. Male A, caught on July 26, was in the middle of molt involving all tracts, with sheathed feathers numerous on the head and chin, back, breast, and both wing and tail coverts. One of the central pair of rectrices was lacking from the old tail. The first primary was about 20 mm. long, about half-sheathed, and the second primary was 12 mm. long and half-sheathed; all the other old remiges seemed present. No good opportunity to study Male A in the field came again until August 24, when the outer pair of rectrices was one-half inch short of full length and the next pair one-fourth inch short. From below, a bare area on the belly was visible. The same traces of molt were seen on August 27, but thereafter the new plumage looked complete. Male C appeared to have finished his molt by August 27, 1959, when he was rediscovered. The unbanded male thought to be Male D was molting and lacked a tail on August 2, but on August 29 it showed only a slightly ragged throat.

Female A, examined on the same day as Male A, July 26, 1959, showed no molt; later sightings of her were too brief to permit observation of plumage. Female B on July 30, 1959, had lost many feathers from the head, neck, and breast but was otherwise still in old plumage. When she was last found, feeding young on August 6, her tail had lost two or three pairs of rectrices and her head was very ragged.

Departure.—Male A was seen and heard nearly daily from late August through September 11, 1959, and Male C was seen through September 15. These dates correspond with those given in Bent (1950:262) for the fall migration, and with Bennett's latest record in Iowa (1917:285). Mrs. Lawrence (1953:70, 74) stated that Red-eyed Vireos remain on territory until going south; from context she was referring to both sexes.

VOICE

Some reference to song frequency throughout the summer appears in the foregoing sections. Bent (1950:259–260) and many others have described the normal song, and the following notes are limited to vocal behavior not found discussed elsewhere. No female was known to sing, but Pitelka and Koestner (1942:103) recorded female song, perhaps connected with nest relief.

Adult "run-on" song.—On three occasions, two of them in the course of this study, I heard an unusual, rambling song, single performances of which lasted ten seconds or more. Adjectives in my notes attempting to describe it are "twanging," "Bobolink-like," "bubbling," "jerky," "squeaky." The volume was at times faint. Twice there seemed to be a complex recurring pattern faintly reminiscent of the typical song of the species, so that in this respect there was a resemblance to rehearsed song in certain young birds. What may have been an intermediate between run-on and typical singing was a performance by Male C on August 28, 1959. The normal song suddenly became hushed and twanging and by the introduction of many new notes achieved a sort of double, improvised, *bel canto* effect.

The first true run-on song I heard near Indianapolis on June 1, 1946, from a male closely accompanying a female, apparently in an early stage of nesting (see Mumford, 1952:230). During the present study, Male D sang as described on the morning of May 26. This was the day I discovered him, and although searches made in the next few days indicated that he was then unmated, he may have had a female on the date the song was heard. Male B sang several run-ons in the early morning on June 16 during the laying period of his replacement nest; he was perched first in the nest tree and then 20 yards from it, ten feet off the ground, and gave the impression of being excited.

It may be this same song which Du Bois (in Bent, 1950:260) describes as "entirely different . . . with loud, harsh squeaks," and Mrs. Nice (1929:16) heard "a squeaky, scolding series something on the order of the song . . . ." White-eyed Vireos often sing protracted, rambling, sometimes faint, catbird-like songs, into which more typical phrases of the species may be introduced. That a comparable vocalization is widespread in the genus, possibly connected with courtship, is suggested by a number of reports (Lawrence, 1953:72; Bent, 1950: *solitarius* 299, *flavifrons* 285, *olivaceus* 335).

Unusual occasions for song.—Male A on July 17, 1958, sang frequently, once arching his back and uttering a normal song in flight. The occasion for this was undiscovered; 36-day old young were probably somewhere near. Male B when caught on July 2, 1959, was wild with excitement and gave a loud mixture of scolding notes and song; when released he sang immediately. Song by the male on the nest, as in many other vireos, has already been referred to; I heard it only once.

Song by young birds.—The sub-song of a juvenile 37 days old has been mentioned. In its length and rambling, twanging character it resembled the adult run-on song, but no pattern was discernible and the singer's species was only faintly suggested by his voice. The single songs of birds about 40 to 45 days old have been described.

Calls.—Both adults give a loud *chee chee* or *cheev cheev* call when alarmed. The rate for continuous calling is 25 per five seconds, but more commonly there are slight pauses so that the number ranges between 12 and 20. A call that I find indistinguishable except in its slow, irregular rate serves apparently to maintain contact within the family. Young give the *cheev* call, but at a higher pitch and less vigorously than do adults until they are about 35 days old.

The long, crying notes of disturbed nestlings have been discussed, as have the chicken-like *peeps*.

Faint calls heard from a male and female in a courtship chase were unlike any mentioned herein, but I cannot describe them.

ENEMIES

The rate of cowbird parasitization, two eggs in one nest of the eight studied, is much below that which one would expect in the light of heavy molestation of the Prairie Warbler here (Nolan, MS) and of the Bell Vireo elsewhere (Pitelka and Koestner, 1942:

100–102; Bent, 1950:260–261; Mumford, 1952:231–232). The vireos did not desert the nest, and I then immediately removed the parasite eggs in order to obtain other data. Egg 2 disappeared from another nest during laying and perhaps was taken by a cowbird.

The predators to which the occupants of three nests succumbed are unknown, but the undisturbed condition of the nests themselves suggests the pilot black snake (*Elaphe obsoleta*) and the black racer (*Coluber constrictor*). These are perhaps the commonest nest predators in scrub habitat here.

The four nests of pairs A and B in 1959 were heavily infested with the mite *Ornithonyssus sylviarum*. Bites of *Ornithonyssus* may have accounted for numerous small, brown, scab-like growths on the tarsi of the nestlings in July; these lesions were about 0.5 mm. in diameter. One nestling when banded had fresh blood at the base of the hind toe. The softer skin of the bodies of the nestlings showed no conspicuous scabs, but I did not think to make a close examination for them. I am indebted to Nixon Wilson for identification of the mites. Pitelka and Koestner (1942:103–104) found nests of two pairs of Bell Vireos infested by this species; in one a nestling died.

REPRODUCTIVE SUCCESS

In summarizing reproduction, the nest parasitized by the cowbird is treated separately. For nests found after laying but containing four eggs or young, clutch size is assumed to have been four. Twenty-eight eggs were laid in seven nests, and 23 eggs (82 per cent) hatched. One clutch of four failed when three eggs disappeared, and in another nest one egg disappeared in the laying period. Of the 23 eggs that hatched in six nests, 16 produced fledglings; that is, 57 per cent of the eggs laid, or 69.5 per cent of those hatched, survived to the stage of nest-leaving. One brood of four nestlings and another of three disappeared. Each of the four successful nests yielded four fledglings.

The nest parasitized by the cowbird was found with one cowbird egg in it; next day it held one vireo and two cowbird eggs, and ultimately it held two more vireo eggs. The cowbird eggs were removed, one vireo egg failed to develop, but two vireo eggs hatched and produced fledglings. The young in this brood of two and those in a brood of four were followed to ages of 35 and 40 days and all survived.

MISCELLANEOUS

Adult weights.—All the following weights are of adults feeding nestlings. Males weighed 9.1, 9.5, 9.5, and 9.9 gm.; these were recorded, respectively, at 8 a.m., June 18; 11 a.m., July 26; 4:45 a.m., June 7; and 7 p.m., July 2. The first two weights are of Male A in the two successive years. Females weighed 9.6, 9.6, 10.5, and 11.0 gm. on the following dates, respectively: 7 p.m., July 2; 4:45 a.m., June 7; 9 a.m., June 18; and 6:30 p.m., July 5.

Measurements.—Wings (chord) of two males were 56.8 and 57.0 mm. long, of two females, 54.0 and 55.2 mm.

Head scratching.—The foot was extended over the wing in one observation of head scratching by a male.

Bill wiping.—A male was seen wiping his bill by scraping it from base to tip on a branch.

Bathing.—The only water on the home ranges was from dew and rainfall. Male B on a dewy morning in July bathed by rubbing against leaves until he was very wet. I have seen *Vireo griseus* do much the same thing; this has also been recorded by Southern (1958:201) in *olivaceus*.

Unusual feeding behavior.—Male B twice caught large black flies or Hymenoptera,

carried them to a branch, and put his foot on them while he hammered them with his bill and picked out soft matter. He then worked on the bodies with his bill and ate them. I once saw a White-eyed Vireo put his foot on a tough spider egg case, and Herrick (1935:229) saw a Red-eyed Vireo hold a caterpillar in this way while battering it with the bill. Skutch (in Bent, 1950:297) reports use of the foot by the Solitary Vireo, but says that the habit "appears to be very imperfectly developed among the vireos." In connection with the presence of the behavior in the Bell Vireo, Chapin (1925) found this species to take a greater quantity of such bulky insects as grasshoppers and the like than any other vireonid whose food items are known. Use of the foot would seem to be correlated with the eating of large, hard insects.

The Bell Vireo occasionally took food from a leaf as it flew past with scarcely a pause. Seizing food in flight has been noted in many vireos and seems especially conspicuous in the Philadelphia Vireo (Lewis, 1921:200).

Wing flicking and tail flicking.—Wing flicking and lateral tail movements associated with courtship and performed by both adults, especially the male, have already been described. Indistinguishable movements were seen in both adults and in juveniles nearing 40 days of age, when nervousness at my intrusion or possibly the excitement of mutual association seemed to be dominating the behavior of the moment. Under these circumstances either the wings or the tail or both were flirted, the tip of the tail traversing an arc of as much as 2½ inches.

SUMMARY

During 1958 and 1959, five pairs of Bell Vireos and an unmated male were studied at Bloomington, Indiana, where the species has probably only recently become established. Members of pairs were color-banded, and two males and one female were present in both years. The habitat was dry open scrub, which may have been selected because in it contact with the White-eyed Vireo was avoided. Breeding pairs were isolated one to a field, although fields were large enough to accommodate more than a single pair. Home ranges, which measured two to three acres, were reclaimed by two males in successive years, and a female rejoined her mate of the previous season.

The birds arrived in early May. A male sang often until he had acquired a mate, after which he became relatively silent for a time. Rapid chases and following were conspicuous during pair formation. A nest was begun no more than five days after a pair was formed. All nests were two to three feet above ground; both sexes built. Construction of first nests seemed to take more than the four or five days required to replace a nest lost to predators. When the nest was finished, the female sometimes began to lay on the next day and once she waited as long as two days before laying; she laid an egg a day for three or four days, probably always in the early morning. The beginning of incubation was irregular but it usually occurred at least one day before the last egg was laid. Males were found to lack incubation patches, so that in their intervals on the nest they sheltered and guarded but probably could not have supplied much warmth to the eggs. Eggs hatched after about 14 days of incubation.

The nestlings, which were naked and one of which weighed about 1 gm. at hatching, were covered and fed by both adults. They left the nest at age 10.5 to 12 days; all members of the brood sometimes left on the same day, but on occasion the departure of an entire brood required 48 hours. Until they became adept at flight the young remained on the home range and were probably separated from each other. At the age of 35 days, when only small traces of the postjuvenal molt remained evident, the broods were gregarious although individuals might perch alone and utter sub-song. Parents still were followed and were begged for food, and the broods remained intact until the

fledglings were 40 days of age or a little older. The young then disappeared. At this stage they were capable of song resembling the adult's.

Second broods were raised; one new nest was begun about seven days after the first brood left its nest. Care of the young in this case occupied the parents through August, by which time the postnuptial molt was virtually complete. This molt began in mid-July in two males, which was earlier than in their mates. In late summer males tended to spend much time in a single thicket, either on the breeding range or as much as 400 yards from it. Song continued until departure in mid-September.

The mite *Ornithonyssus sylviarum* was an abundant ectoparasite in 1959.

Seven of eight nests held clutches of four; the eighth, which held three, was the only one parasitized by a cowbird. Of 28 eggs laid in the seven nests, 23, or 82 per cent, hatched and 16 young, or 57 per cent, left the nest.

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Indiana University, Bloomington, Indiana, April 1, 1960.

AGONISTIC BEHAVIOR IN THE HOUSE FINCH
Part I: ANNUAL CYCLE AND DISPLAY PATTERNS

By WILLIAM L. THOMPSON

The primary purpose of this study is to describe the agonistic behavior of the House Finch (*Carpodacus mexicanus*) with an emphasis on aggression and dominance relations. By "agonistic behavior" is meant fighting or hostile behavior, including avoidance and fear reactions which may occur in hostile encounters between birds. The annual cycle of House Finches for the area near Berkeley, California, is described briefly as background for the discussion of behavior. Social hierarchies of wild and caged birds are analyzed, and factors involved in their determination are discussed. Additionally, to determine the effects of sex hormones on aggressive behavior and on social hierarchy, the behavior of male castrates both with and without treatment with testosterone were compared with the behavior of intact males; these results will be reported elsewhere.

Collias (1944) summarized the literature on aggressive behavior in vertebrates, and an overall review is not called for here. Probably the most conspicuous expression of aggressiveness in wild birds occurs in the course of territorial defense. Several recent reviews summarize the extensive literature on territory in passerine birds (Nice, 1937; Hinde, 1955; Tinbergen, 1957; Carpenter, 1958).

Another basic aspect of aggressive behavior is the formation of a social hierarchy or peck order. This was first described by Schjelderup-Ebbe in 1922 for chickens, and the extensive literature relating to their social behavior has been summarized by Wood-Gush (1955). Masure and Allee (1934) extended the study of social organization to pigeons and parakeets. Shoemaker (1939) described a peck order in small flocks of caged canaries. Since 1940, peck order has been described for several other passerine species, both as captives and in the wild. Odum (1941–1942) and Hamerstrom (1942) found a definite social hierarchy in flocks of wild Black-capped Chickadees (*Parus atricapillus*); Colquhoun (1942) describes a similar situation in wild Blue Tits (*Parus caeruleus*); Hinde (1952) includes data on social organization and on specific patterns of aggressive behavior for the Great Tit (*Parus major*) and other parids; Sabine (1949, 1959) found a well-established peck order in the Slate-colored Junco (*Junco hyemalis*), Oregon Junco (*Junco oreganus*), and Tree Sparrow (*Spizella arborea*); Hinde (1955–1956) mentions peck order and aggressive elements in the courtship behavior of several fringillids; Tordoff (1954) studied the peck order of a small winter flock of captive Red Crossbills (*Loxia curvirostra*), Nicolai (1956) of captive Bullfinches (*Pyrrhula pyrrhula*), and Marler (1956) of captive and wild Chaffinches (*Fringilla coelebs*). In addition, a series of recent papers in the field of comparative ethology too numerous to list here have dealt in part with the agonistic behavior of various species, particularly passerines.

MATERIALS AND METHODS

Observations of both wild and caged birds form the basis of this report. Observations of wild birds were made in Strawberry Canyon on the University of California campus, at a feeding station in a residential area of Berkeley, and at the Hastings Natural History Reservation, Carmel Valley, California. In addition brief observations were made at various other places throughout the San Francisco Bay area. Birds were watched using 7 × 50 binoculars. Notes were recorded directly in the field at the time of observation. No specific routine of observation was followed, and length of time spent observing depended largely on the activity of the birds and on the schedule of the observer.

Wild-captured, color-banded, adult House Finches were used for observations of behavior in captivity. In 1954–55 a flock of nine birds was placed in a cage of ½-inch mesh screening seven feet long, three feet wide, and three feet high. The back and floor were wooden. Several wooden perches were

placed at varying heights and positions in the cage. A wooden nest box, open in front, was used during the winter as a roost, and during the spring as a nest site. The cage was located in a shelter in the courtyard of the Life Sciences Building on the University of California campus. The shelter was provided with a white-washed glass roof and hardware cloth walls. The birds received direct sunlight for at least part of the day throughout the year. Length of day and temperature were therefore approximately the same for the caged birds and for wild birds in the Berkeley area, although light intensity was somewhat less in the cage than out-of-doors. The birds were observed through a "one-way glass" window at one end of the cage.

In 1957–58, four cages eight feet high, four feet wide, and four feet long were employed. Three of the four cages contained four pairs of birds, while the fourth contained one male and two females. These cages were located in Strawberry Canyon on the University of California campus, in an area inhabited by many wild House Finches. The cages were built under live oak and laurel trees and were shaded during most of the day, but some direct sunlight did reach the birds. Wooden perches were placed at varying heights. Shelter was provided by an 18-inch wide wooden roof over one side of the cage. The birds were observed through a three by five-inch opening at one end of each cage.

At all times, water, gravel, and a seed mixture consisting of canary seed, oat groats, and rape were available. Several times each week lettuce and apple or orange slices were also provided. During the spring and early summer, dry grass, string, and fresh green vines were placed on the floor of the cages, and were used by the birds as nesting material.

Three eight-day-old sibling House Finch nestlings were hand-reared. At first they were fed a soupy mixture of milk, cooked egg yolk and whole wheat bread crumbs, and were kept together in a covered box. When two weeks old, they were placed in a wire cage, and canary and rape seeds were introduced into the food mixture. When the birds were three weeks old, the egg and milk mixture was discontinued and they were fed a mixture of water-soaked bread, and canary and rape seed. A dry seed mixture was placed in the cage, along with daily rations of lettuce and/or apple, but the wet mixture continued to be available until the birds were ten weeks old, by which time they were feeding almost entirely on the dry seed, fresh fruit and greens.

A standard form was used for recording aggressive encounters among caged birds. A double-columned sheet was used to record the color-band combinations of the attacker and the bird which was attacked, and which avoided the attacker. The form which was used in 1954–55 provided separate columns for different perches in the cage in order to reveal any territoriality in relations between individuals in the cage. Since none developed no provision was made in later forms for the localization of aggressive encounters in different parts of the cage. Occasional observation sessions were devoted entirely to the recording of descriptions of postures, call notes, and activity patterns. The length of observation sessions varied from 10 to 60 minutes. Observations were made both in the morning and afternoon in 1954–55, but only in the morning in 1957–58. Since there were four cages to be watched in 1957–58 the sequence of observation of the cages was varied so that each cage was observed at a different time on consecutive mornings. In this way the effects of morning cycles of activity and inactivity were reduced, and the records for different cages were made more comparable.

An encounter between two individuals was recorded as an aggressive encounter if one either pecked the second, or if it threatened the second by moving toward it as if to peck, or performed one of the aggressive intention movements described subsequently in the text, or if it supplanted the second individual. Often it is possible to determine the dominance relationship between two individuals by the avoidance of one by the other, but this is not so reliable an indication of subordinate position as an actual flight or avoidance of a peck or threat by another bird.

ACKNOWLEDGMENTS

I wish to express my thanks to Frank A. Pitelka for his helpful suggestions and criticism throughout the course of this study. I wish to thank, also, Peter Marler, Howard A. Bern, Alden H. Miller, and Benbow F. Ritchie for their advice. To Mrs. Harold P. Henningsen for help in obtaining many of the experimental birds, to Retta M. Thompson for help in many facets of research and preparation of manuscript, to Max C. Brewer for aid with field observations, to J. Mary Taylor for help with some of the photographs,

and to other members of the Department of Zoology and the Museum of Vertebrate Zoology who have helped in many ways, I extend my sincere thanks.

This paper represents a condensed version of a thesis deposited at the University of California, Berkeley, California. References to "Thompson MS" pertain to the thesis, from which particulars may be obtained.

HABITAT AND FOOD

A compact statement of habitat of the House Finch is given by Grinnell and Miller (1944:454). Its geographic distribution has been mapped by Salt (1952). Water needs of House Finches and their adaptability to desert and dry summer regions has been studied by Bartholomew and Cade (1956). Eating of salt by House Finches has been noted in the literature (Peterson, 1942; Linsdale, 1957) and also by the writer.

House Finches are primarily seedeaters (Roessler, 1936) but they also eat fruit, and are considered a pest by fruitgrowers. Beal (1904) reported that the animal intake of House Finches amounts to little more than three per cent of the yearly food intake. It consists primarily of plant lice (aphides). Probably these insects are taken by accident along with vegetable material. Large numbers of House Finches are attracted to fields of blooming and fruiting wild mustard (*Brassica campestris*) and radish (*Raphanus sativus*) in the spring. In the fall, great numbers congregate at stands of ripe thistle (*Cirsium*) and other composites. The race from San Clemente Island makes use of cactus fruit as a food source (Grinnell and Miller, 1944).

House Finches usually nest in dense foliage and often build in ivy under the eaves of a building, if such a site is available. In the absence of dense foliage or a man-made structure, they may nest in crannies on cliffs. In many ways House Finches are similar to House Sparrows (*Passer domesticus*) in their nesting requirements, and the two species may compete for nest sites (Evenden, 1957; Gilman, 1908). Keeler (1890) wrote about the House Finch that "wherever it is scarce the English Sparrow is proportionately abundant and it seems not impossible that one may supercede the other in course of time." Gilman found House Finches able to defeat House Sparrows unless outnumbered by them, but observations in Berkeley have indicated that it is more often the somewhat larger and heavier House Sparrow which wins fights between the two species.

ANNUAL CYCLE

Agonistic behavior may be observed throughout the year among wild House Finches. It occurs primarily at resting or roosting sites, where several birds are perched near each other preening, calling, or singing. It occurs less frequently while birds are feeding in the open. Even when many birds are feeding in close proximity, as in the large feeding aggregations of adults and juveniles in late summer, there is very little aggressive behavior. Agonistic behavior does, however, take place regularly at feeding stations where food is available to only a few individuals at a time.

In early spring when pairs are forming, aggressive behavior reaches a peak. Increasingly, males become intolerant of other males perched near them. Males, when they have secured a mate, defend the area around the female, in the same way as Twining (1938) describes for a race of the Gray-crowned Rosy Finch (*Leucosticte tephrocotis*). For the most part this amounts only to an increase of individual distance, and the degree to which such an area is defended varies from time to time with any individual. A bird which is resting or preening near its mate may tolerate other individuals or pairs within a few feet, and then, after stretching, yawning, and rousing itself, it will begin to patrol the vicinity, chasing away other House Finches, without any sort of evident provocation on their part.

This peak of aggressive activity continues through the selection of a nest site and the construction of the nest, but it begins to wane by the time the nest is completed. The area around the nest is defended rather sporadically and weakly. Vigorous displays are rarely observed in territorial defense. Usually the defender merely flies to a perch near the intruder and sits until the latter moves away. There are no sharp territorial boundaries, such as are found among Song Sparrows (*Melospiza melodia*), Snow Buntings (*Plectrophenax nivalis*), and many other passerines. Once incubation has begun there is little territorial defense, and it is therefore possible for nests to be built within a few feet of each other, with little or no interference from neighbors if they are in different stages of the breeding cycle.

The distance from the nest to the farthest point from the nest which is defended may be taken as a rough approximation of the radius of the territory. On the basis of territory defense in six nests during the period when territory defense was most vigorous, the average radius was 14 feet, the range 6 to 30 feet. This would give an average territory size of 642 square feet. This figure may be compared with approximately 158 square feet for the House Sparrow (Owen, 1957) which has similar semi-colonial nesting habits and indefinite territorial boundaries.

In the remainder of this part of the paper, particular phases of the annual cycle and the repertoire of displays will be described. In part II, agonistic behavior in caged birds and its significance in social and broader ecological contexts will be considered.

Flocking and movements.—During winter, aggregations of House Finches may be observed in rural and suburban areas. Groups of four, five, six or more birds are sometimes seen perched a few inches apart on power lines beside a highway. In towns, the clumping of birds is less noticeable, although there may be small aggregations at choice feeding areas or favored roosting sites.

The relative sedentariness of local populations of House Finches can be shown best by taking available banding records and analyzing them for evidence of long-distance movements as between breeding and nonbreeding seasons. Records of the recoveries of banded House Finches from 1923 through 1958 in files of the Fish and Wildlife Service were examined for this purpose. Table 1 shows the latitudes at which the 6004 recovered or recaptured House Finches were banded. Most (96.8 per cent) of these were recaptured at the place where they were banded. Column two presents the percentage of individuals that were recaptured or found dead somewhere other than the place where they were banded.

Banding records show that House Finches have been banded in the northern part of their range (up to 48°N) throughout the year, but this does not entirely rule out the possibility that some individuals may leave the breeding area in winter. If those banding records are selected in which one date, either of banding or recovery, falls within the breeding period (March through July) and in which the second date, again, either of recovery or banding, falls within the nonbreeding period (August through February), it should be possible to rule out the likelihood of recaptures of any individual within a single breeding or wintering period. Such recaptures would tend to obscure any evidence of long migratory movements of the population as a whole by emphasizing the percentage of individuals that remain on their breeding area. Column three lists the record of birds banded and recovered in opposite seasons at each latitude for which there are banding records.

If the northern populations tended to migrate south during the winter, the percentage of foreign retraps should be markedly higher for the selected group of birds than for the total except where the numbers in columns one and three are about the same, as at latitudes 50° and 49°N. The percentages are in general not markedly higher for

Table 1

Numbers of Birds Banded at North Latitudes and Distances of Recovery from Place of Banding

Latitude (°N)	Total banded and recovered	Per cent recaptured elsewhere	Banded and recovered in opposite seasons	Per cent foreign recaptures	Longest distance traveled (miles)	> 200 miles	100–200 miles	50–99 miles	25–49 miles	10–24 miles	5–9 miles	1–4 miles
50	1	0	1	0								
49	10	0	9	0								
48	97	0	49	0								
47	0	0	0	0								
46	2	0	1	0								
45	1	0	0	0								
44	8	0	7	0								
43	0	0	0	0								
42	2	50.0	0	0	51			1				
41	4	25.0	2	50.0								
40	133	2.3	41	7.3	15					1		1
39	54	1.9	18	0	9						1	
38	254	1.6	85	1.2	98			1			3	
37	451	4.9	210	6.7	290	1	1	2	3	3		9
36	20	0	11	0								
35	42	16.7	12	6.7	18					1	5	1
34	4261	2.6	2023	3.5	800	6		3	11	24	39	26
33	353	1.1	158	0	87			1				3
32	311	0.6	125	1.6	680	1		1				

this selected group, and furthermore the percentage of foreign recoveries does not increase toward the northern end of the range as would be expected if these northern populations were migratory. Those latitudes which do show a high percentage of foreign recaptures are represented by small samples and the high recapture percentage is probably due to chance. It is true that the banding records do not give an adequate sample of the total House Finch population, since the northern part of its range is poorly represented. Also, recoveries of banded House Finches in proportion to the number banded are very few at any latitude. The larger proportion of recovered birds toward the southern end of the range is undoubtedly a reflection of the greater number of banders in the southern part of the range, particularly in the San Francisco Bay area (37°N) and the Los Angeles area (34°N).

The available evidence indicates that House Finches generally remain on or wander about near their breeding area during the autumn and winter months rather than migrate over a long distance to a wintering place farther south. The few instances of a very long distance (over 200 miles) between the place of banding and the place of recovery may have resulted from man-provided transport.

Pair formation.—In areas such as Strawberry Canyon where House Finches are not winter residents, females become associated with males about a week after males become established on their breeding areas and begin to sing frequently. Males and females fly together and perch together. Since none of these wild birds was banded, it was not possible to determine whether the same birds remained together. About the time the females appear, the males begin to chase each other. Two males may sing from opposite sides of a tree. Soon one may hop across to the other side and supplant the other on his

perch in the same tree. The first may not molest him further. Sometimes, however, the dominant individual will chase the other to another tree. During these chases the birds give a short, staccato call note, repeated in rapid succession. Females become more constantly associated with particular males, and after pair formation has occurred, the two individuals are almost always together until egg laying and incubation.

The details of pair formation are not clear. Since the males do not stake out territories and remain on them until a female appears, it is impossible to observe a wild male or female House Finch continually during this or any other phase of the annual cycle. Pair formation probably takes place as in other birds which mate in winter flocks (Lack, 1940:279), that is, "the members of a pair gradually come together, using many small interrelated mutual actions, with intervals when they move apart again" without either member of the pair appearing to subdue the other, that is, without any simple "sexual dominance." Bergtold (1913) suggested that House Finches remain mated over the winter because he saw the birds in pairs at feeding stations in winter. In Berkeley the close association of the pair so striking during the breeding season is not at all evident during fall or winter. Caged birds do seem to retain some remnant of the pair bond, and billing has been observed during late fall, even between male castrates and intact females. Here it appears that habit and forced proximity may be motivating influences.

In town where both males and females are present through the winter it is difficult to establish the presence or absence of a continuous recognition of the mate as such. In the Coast Range foothills, however, there is some indication that the pair bond is not continuous from year to year. As mentioned above, males begin to appear on breeding areas in mid-February, followed a week or so later by the females. This difference in arrival time would suggest that the birds are not paired when they arrive on the breeding area.

At this time males and females associate in small groups, and the membership of any one group appears to be fluid. Within a few days, however, males become associated with certain females. It is common to see one female accompanied by two males. The males often show no hostility toward each other at first. Frequently the female is the leader in these threesomes. The characteristic flight formation is single file. Soon one male begins to attack the other, and finally only one male remains with the female.

These early stages of pairing are not detectable among caged birds because the individuals are forced to be together and to perch nearer each other than is usual in the wild. Beyond this stage, however, observations of captive birds have helped considerably to fill in the picture. After a few weeks of close association the members of the pair begin a mandibulating activity or billing ("kissing" of Conder, 1948) which leads to courtship feeding. As is true in other phases of the breeding cycle, finches in Strawberry Canyon begin courtship feeding later than do those in town. Conder (1948), in describing the development of courtship feeding in the Continental Goldfinch (*Carduelis carduelis carduelis*), distinguishes four stages which follow each other at intervals of about two days: (1) kissing (or billing), (2) female crouched while kissing, (3) mock feeding, and (4) true feeding. A similar sequence of developmental stages can be observed in House Finches.

The first evidence of pair formation in captive House Finches is billing, accompanied by soft twittering. The male leans toward the female, or *vice versa*, and gently pecks at the closed beak. Usually the bird being pecked leans slightly away from its mate, indicating an avoidance tendency still remaining. Later the birds lean toward each other, both open their beaks slightly, and the male may insert his into that of the female. In the House Finch the "kissing" gives way to mock feeding before the female crouches. Still later the male accompanies this mock feeding with regurgitating movements of the

throat, but no food passes into the female's open mouth. At this time the female usually begins to beg from the male, assuming the customary passerine begging posture and giving loud, rapidly repeated call notes, almost in the same rhythmic pattern as the male song, but in an apparent monotone. The tarsometatarsus is held almost parallel to the ground, the tarsal joint flexed more than usual, and the tail may be lifted 35° to 45° above horizontal or may sometimes be held horizontal. Often the tail is flicked vertically in rhythm with the calling. When this behavior pattern first appears, the female may stretch her neck toward the male, having her beak slightly opened and her head about on the same level as her shoulders. Later in the development of courtship she retracts her neck and tilts her head almost vertically so that the male points his beak downward to feed her. At about the time of nest building, the male actually feeds the female regurgitated material, just as both parents later feed the young. The calling is continued while the male is feeding the female, but the sound becomes very faint while he is stuffing food into her mouth. When the birds are not visible, it is possible to detect feeding by the periodic, sudden muffling of the call note, followed by a rise in the dynamic level after the female swallows. The male usually regurgitates and thrusts his beak into the open mouth of his mate several times during a single feeding, and the begging call of the female becomes a sequence of alternating groups of loud and soft call notes.

A case of mistaken feeding by the male may shed some light on the combination of stimuli adequate to release feeding in the male. A mated pair was observed feeding at a trapping station. The female was caught and began struggling to escape. She gave a low-pitched *chip-chip-chip* call, slower than the usual twittering of courtship feeding, but of similar quality. She frequently looked up at the top of the trap. Her beak was open because of the heat, and her wings, held slightly out from the contour feathers, fluttered periodically during her struggles to get free. Her mate became noticeably excited, hopped around the cage giving a version of the mild alarm call, then hopped onto the cage, peering down at her. Her posture in the cage resembled vaguely that of a begging female (body crouched, head tilted back, beak open, tail slightly spread, wings drooped and fluttering), and this apparently provided an adequate stimulus to cause the male to feed her. He began to twitter and attempted to feed her through the screen of the trap roof, actually regurgitating. The female did not respond to his attentions, however, and he swallowed the food again, then wiped his beak. At this point, he was startled and flew away, whereupon the female was removed from the trap.

Nest building.—Pairs make investigating forays to prospective nest sites, then frequently return to a communal roosting tree to rest and preen for a few minutes before leaving to feed or look at nesting places again. In the Poultry Husbandry area of Strawberry Canyon, a single elderberry tree served as a communal resting place where several pairs of House Finches, along with Brown Towhees (*Pipilo fuscus*), Song Sparrows, and goldfinches, rested, preened, and sang. The birds did not, however, roost there at night and no nests were built there.

It appears that the female makes the final choice of nest site. The male may lead the female to several possible nest locations, sometimes carrying nesting material, but often he merely follows her as she moves from place to place examining sites which appear to be of general suitability. Sometimes the female carries nesting material while inspecting nest sites. Although there is considerable variation in the kind of place chosen by House Finches for a nest, it is usually built under the cover of a roof overhang or in dense foliage. One of the commonest nest locations is an ivy-covered wall, the nest often being built just under the eaves. A drain pipe or rafter just under a roof overhang is also a frequently used location. Where sites are not available on or in man-made buildings, dense foliage or cliffs may be chosen.

When a nest site is picked the female begins to collect nesting material. A great variety of materials may be used. It appears that the birds utilize almost any pliable material of appropriate size that is locally abundant. Dry grass stems, roots or leaves, and plant fibers stripped from the woody stalks of weeds or bushes are commonly used in the Berkeley area. Green vines and sprigs of Scotch broom (*Cytisus scoparius*) blossoms have also been found as nest components. Hair, feathers, cotton, string, thread, soft paper, frayed cigarette filters and very fine plant fibers may be used for the lining.

During the early part of the breeding season both males and females may be seen picking up twigs or grass, leaves, stems, or other material, but dropping them almost immediately, or carrying them only a short distance. This sort of behavior was also described for the Song Sparrow by Nice (1943). Captive, hand-reared juvenal birds perform the same action, picking up pieces of paper or feathers from the floor of their cage. In the male this behavior is continued through nest construction, whereas in the female it matures into actual nest construction.

The male accompanies the female on each trip she makes and may sit watching her, peck at the ground as if eating, or collect nesting material himself. Only rarely does he carry material to the nest, and then it is apparently not used in construction. My own observations differ in this respect from those of Evenden (1957) who reports active participation by males in nest construction. Grinnell and Linsdale (1936) suggest nest building by males. Their description of the male accompanying the female as she collects nest material, picking up material himself and sometimes carrying it to the nest, are in accord with my own, but I have never seen the male deposit the material carried in his beak on the nest. Usually he drops any object he has picked up before arriving at the nest, or he may take it into the nest, then come out still carrying it. Captive, adult males have been observed to follow the female onto the nest she is building, pick up the piece of grass she had just deposited, and fly off with it, sometimes returning it, sometimes not.

The frequency with which females bring material to the nest varies both throughout the day and with the stage of construction of the nest. During the early part of nest construction the female of pair 4 (1958) returned to the nest at intervals of one to three minutes for most of the morning. Spurts of fairly intense nest building alternated with periods of rest, particularly in the afternoon hours, when the frequency of carrying material to the nest dropped off considerably. Two days later, when the nest was about finished except for the lining, female 4 returned every ten to fifteen minutes, with some shorter intervals during spurts of intense building. Female 3, whose nest was discovered while she was lining it, likewise returned to the nest about every ten minutes, remaining on it from one to five minutes to work the plant fibers into the nest cup. Female 8, in the early stages of construction, brought nesting material on the average of every 3.5 minutes for 30 minutes or so, then was away for 15 to 20 minutes, after which she resumed her building. The data are insufficient to make more than an estimate of the time consumed in nest construction, but it appears that about four to seven days elapse between the beginning of nest building and the laying of the first egg. After the first egg or several eggs are laid, materials may be added to the nest.

Three caged females built complete nests. One of these repeatedly attempted to construct a nest in one corner of the cage, but the grass kept falling off the platform. A larger support was provided and a pile of grass crudely arranged in the form of a nest was placed upon the platform. The female took possession almost at once, crouching and twisting her body in short arcs to mold the cup and rim, and adding a lining to the cup. Seven days later the first egg was laid. Similar crude nests were provided in each of the other cages, but in every case the pair owning the nest site pulled out this artificial nest,

even if it was firmly attached to the platform. Some individuals later began construction on their own, some did not. One female repeatedly attempted to construct a nest. At times she would bring a piece of grass to the nest site, place it on the pile of material already in place, go off the nest, approach it by another route, and take off the same piece she had just deposited. This deposition and removal of a single item was continued for several minutes, then the material was dropped to the ground, and the bird fed or preened for a few minutes before resuming her attention to the nest. She frequently performed the crouched, twisting movements of molding the nest cup, even when there was very little material present to mold. Indeed, she sometimes appeared to be performing the movement on the bare platform with only a few isolated pieces of grass at the edge.

This same female was plagued by the depredations of her mate. He followed her onto the nest and disarranged the material she had just arranged, sometimes removing some of it. Both birds inspected the nest frequently without adding or removing anything. This nest was never completed.

House Finches almost always build a complete new nest for each brood. There are records of their use of the nests of other birds. Shepardson (1915*a*, 1915*b*) notes the laying of House Finch eggs in nests of the Black Phoebe (*Sayornis nigricans*), Cliff Swallow (*Petrochelidon pyrrhonota*), and Hooded Oriole (*Icterus cucullatus*). Robertson (1931), Hanna (1933) and Hensley (1959) recorded the parasitization of House Finch nests by cowbirds.

Copulation.—Copulation begins during the later stages of nest construction, several days before the first egg is laid, and recurs several times each day until the clutch is completed. It usually takes place in the early part of the morning. Marler (1956) describes its occurrence in the Chaffinch as in the very early morning shortly after sunrise. House Finches in Strawberry Canyon do not generally become very active until an hour or so after sunrise. Blanchard (1941) reports the occurrence of copulation in the White-crowned Sparrows (*Zonotrichia leucophrys*) throughout the day but most frequently during the half hour before sunset.

Egg laying and incubation.—Eggs are laid early in the morning. They are laid on consecutive days until the complete clutch of three to seven eggs is finished. Bergtold (1913) reports the average clutch in Colorado as being four with a range of two to seven. Evenden (1957) gives 4.2 as the average clutch size, with a range of four to six, on his study area in Sacramento, California. The nests examined in Strawberry Canyon averaged 4.7 eggs per clutch, with a range of three to six.

Bergtold (1913) mentions a special call used by the female while laying and distinguishes this from the call note given by the female while she is incubating. I have been unable to make such a distinction.

Michener (1925) reported a case of polygyny in which a male and two females "worked together" to build a nest. Ten eggs were laid; one of them was crowded out of the nest. Finally one female left the area and six of the eggs hatched.

On the day the first egg is laid the female may spend some time on the nest, apparently incubating. Certainly incubation begins before the last egg is laid. Evenden (1957) found the female on the nest only very early and late in the day during the early part of the laying period, but as the clutch neared completion she remained on the nest for increasing periods of time and sometimes began full-time incubation the day before the last egg was laid.

There is sometimes a marked difference in the size of young House Finches in a single nest, although Evenden did not find such a difference in the nests he studied. It is possible that this size difference, when present, is due to brief intervals of incubation

before the clutch is finished. Precise hatching dates and times are needed to answer this question about House Finches. Nice (1943) reported that the female Song Sparrow usually begins incubation the day before the last egg is laid. Marler states that the female Chaffinch may sit on an incomplete clutch up to 30 minutes after bringing material to the nest.

On the nest the female utters a soft *chee-chee-chee, chee-chee-chee* continuously, the notes characteristically in groups of three with pauses between groups. There is some variation in pitch, but the general impression is that of a monotone. The dynamic variation, however, is more marked. The reason for this variation is not apparent. The call seems to serve as communication between the female and her mate. On two occasions incubating females were heard calling softly in this way, then increasing both volume and to some extent frequency of the notes. When caged females produce this call, it usually incites the male to strenuous chasing of the other birds in the cage.

Bergtold (1913) gives the incubation period for Denver as 14 days, sometimes more (up to 17), rarely less (13). Keeler (1890) reports the incubation period as 13 days. Evenden (1957) records a mean incubation period of 13.27 days, with extremes of 12 to 16 days.

While the female is incubating the male spends most of his time feeding and preening, often in company with other males. Some females whose first nesting attempts have been unsuccessful or which have not begun nesting may join these largely male assemblages in feeding areas often some distance away from the nest location. These assemblages resemble those of autumn and winter in their loose organization. One such company of 20 to 25 birds observed at the Hastings Reservation in June, 1958, moved as a loosely integrated flock feeding on the ground in a recently cut field. There seemed to be units of two or three birds which stayed close together. Feeding and resting periods were broken for males by occasional trips to an elevated perch to sing. Once the entire group flew up, circled back and alighted on power lines and adjacent trees. After a few minutes of singing and preening the flock, composed primarily of males, but with a few females as well, moved back to the ground to continue feeding. First one bird, then several, then a few more flew down from the elevated perches, until the entire group was on the ground again.

During the incubation period the male stays away from the vicinity of the nest most of the time, and almost never is heard to sing near it. He does come regularly to feed the female, at least during the early part of the incubation period. In most observed instances the female did not leave the nest until called from it by the male or unless she was frightened off. The male flies to a perch a few feet from the nest and calls *cheep, cheep*, slowly and softly. Some females fly out at once to be fed, but others wait for several minutes before they leave the eggs. In only a few instances was the female fed on the nest. Usually the male accompanied the female back to a perch near the nest but seldom went to it himself. If for some reason the male did not come back within about an hour, the female might fly off on her own to look for food, or she might remain sitting for a longer time than usual. One female was observed to stay on the nest for two hours. Her mate rarely summoned her to be fed, and she frequently left alone. This individual was well along in incubation, and it may be that the male attends the female less regularly at this time. There is considerable variation from pair to pair in this regard.

Most pairs begin nesting and hence reach the incubation stage at about the same time. The males tend to aggregate at feeding areas during the intervals between feeding of females at the nest, and perhaps for longer periods if, as has been suggested, this regular feeding of the female breaks down in the latter part of the incubation period. Some pairs begin nests but do not lay eggs or may not incubate them if laid, and these

pairs may join the male flocks to forage. During the breeding season these sizeable flocks are often encountered in open fields or other suitable feeding areas.

At this time of year, also, communal roosts in dense foliage may be used by the males and non-nesting females. The male of a pair may roost near the nest, but more often he roosts at some distance from the nest, as Evenden (1957) points out. On the Strawberry Canyon study area, the dense foliage of three *Eugenia* trees served as a roosting place for more than 20 birds a night during late spring. Individuals slept within three inches of each other, and there was much chattering and supplanting as the birds settled down just before dark.

Hatching and care of young.—Evenden (1957) notes that the female remains on the nest much of the time for the first few days after the young hatch. This was also true for nesting observed in this study. After this time, however, the young are brooded very briefly, if at all, at the time of feeding. At two nests beyond brooding stage, at which observations were made intermittently, feeding occurred about every 30 minutes (15 records of intervals). At some nests the young are fed almost exclusively by the female, whereas in others the male may also take an active part. The male fed the young at a nest which was watched for ten hours, starting at 8:10 a.m. on April 23, 1955. The nest contained five young about seven days old. The female fed 10 times, the male 13. Feedings occurred at about 25-minute intervals. The interval away from the nest was about 55 minutes for both male and female (57.6 and 54.7 minutes, respectively). The female remained on the nest to brood the young for an average of 5.1 minutes, whereas the male remained at the nest an average of less than a minute. Evenden also found both parents feeding, but Keeler (1890) reports only the female feeding young. The male of one pair in Strawberry Canyon fed the young alone after his mate disappeared when the nestlings were a week old. The nestlings are fed entirely by regurgitation, as are the begging adult females. Apparently no insect or other animal food is brought either to adult females or to nestlings. While the parent is feeding them the nestlings produce a rapidly repeated, high-pitched, but soft, *cheep, cheep* call.

Evenden (1957) found young leaving the nest from 12 to 18 days after the date of hatching. His observations give an average initial flight of 49.3 feet with extremes of 12 and 125 feet and an average gain in altitude of 1.6 feet. My own more limited observations were as follows:

Date	Distance	Height gain or loss
June 11	15 ft.	+ 3 ft.
June 13	15	+ 3
	40	+ 10
	15	− 1
Averages	21	+ 3

In each instance the bird flew to a nearby perch. In one, the fledgling followed the female parent from the nest and settled down near another adult. The initial flight distance undoubtedly varies with the surroundings of the nest. The young are not usually enticed off the nest, but they may follow one of the adults as it leaves. In three instances, the young left with no apparent external provocation. After leaving the nest, fledglings begin to *cheep* softly. They beg from any adult which comes near them. They hop or fly directly toward the adult, or even toward other juveniles.

Post-breeding activities.—It is not known what happens to the young just after they leave the nest, but they probably do not join large feeding flocks during the several weeks when they are fed by both parents. Later on juveniles and adults may assemble where food is plentiful. On July 8, 1958, the hills east of the Poultry Husbandry area,

on the south side of Strawberry Canyon, were covered with dense stands of thistles bearing ripe heads. About half an hour before sunset a large aggregation of 200 to 300 birds was seen feeding on the ripe seeds. Most of them were adult and juvenal House Finches, together with a few Brown-headed Cowbirds (*Molothrus ater*) and American Goldfinches (*Spinus tristis*). The ratio of adult male-plumaged to female-plumaged House Finches was approximately one to five. Birds with female plumage may be either adult females or juveniles of either sex. There are differences in the degree of wear of the feathers of an adult female and a juvenile at this time of year, but from a distance these differences are not apparent.

Every few minutes a small segment of the aggregation, 10 to 20 birds, would become alarmed and fly up, but they would settle down almost immediately a short distance from their original feeding locality. Although the intervals between individuals were short, only two to four inches in many cases, there appeared to be no aggressive behavior whatsoever—no pecking, no supplanting.

After sundown the assemblage began to disperse. Singly and in groups they left the feeding area, flying down the canyon, some going toward Berkeley, others going over the southwest ridge toward Oakland. One large group of 50 individuals and other small groups of two or three, flying down the canyon toward town, met and passed other birds flying up the canyon to the feeding area.

Salt (1952) mentions that the large autumn aggregations may move to elevations higher than their breeding areas and then move back down as winter progresses. During mid-October the number of House Finches to be seen in Strawberry Canyon decreases markedly, and by November the species is scarce. In residential areas of Berkeley, Oakland, and adjoining towns, the House Finch population seems to change little with the seasons. Birds in town may spend the winter on or near their breeding area and do not gather in large flocks, although small groups of birds are often seen. Usually rural flocks, also, are of small size, perhaps because the local concentrations of food which attracted large numbers of individuals into small areas in the fall are not available and because food is more widely dispersed during the winter.

Molt.—The Micheners (1940) give the period of molt in the vicinity of Pasadena, California, as May 1 to late November. In the Berkeley area, however, molt appears to be more restricted to the period from September through early November. For an individual the molt lasts about 105 days, varying from 90 to 120 days. Most males assume the adult male plumage at the time of the postjuvenal molt, but some (van Rossem, 1936) retain the female pattern through the first year. The latter condition is more typical of the other members of the genus, including the American species, the Purple Finch (*Carpodacus purpureus*) and the Cassin Finch (*C. cassinii*), as well as most Eurasian species (Dementiev, 1954).

Figure 1 summarizes the sequence of events in the annual cycle of the House Finch in the San Francisco Bay area.

Comments on nesting success and timing.—Of 11 nests begun in the Strawberry Canyon study area, 10 were completed. Eggs were laid in at least eight of these, and incubation was begun in all eight. All but two nests were abandoned after a few days of incubation. Eggs had disappeared from three when they were found to be abandoned. Small mammal nests were constructed over three of the deserted structures, in one nest on top of the eggs. More hair, paper, fine plant fibers, and other soft materials were added to the lining and a roof was constructed of the same materials. The owners were never identified. Probably feral house mice (*Mus musculus*) were responsible.

The eggs of only two nests were known to hatch. The young of one nest fledged but were fed rather irregularly by the male parent only and left the nest prematurely, ten

days after hatching, remaining for several days in vines below the nest. Their fate and that of the other young was unknown.

It is possible that high density of breeding pairs on an area so small as that used in Strawberry Canyon made nest robbing easier for whatever it was that destroyed clutches and caused nests to be abandoned. Steller Jays (*Cyanocitta stelleri*) are abundant in the area and are on record as nest robbers (Bent, 1946) although not specifically as robbers of House Finch nests. Cats are common, but most nests were probably out of their reach. Nests were located on an average of about 30 feet apart, with some in clusters much closer together. Of the nests begun during the five-year period of his observation, Evenden (1957) found 48 per cent destroyed or abandoned.

During 1958 there was evidence of second broods at the Hastings Reservation, but in the Strawberry Canyon study area there was no evidence of more than one nesting, although Keeler (1890) reported that two broods are produced in the San Francisco Bay area. For several weeks after most of the nests were abandoned near the end of April, House Finch activity in Strawberry Canyon was greatly reduced. Very few birds were in evidence, and very little singing was heard. On May 22, however, there was a heavy rain during the night. The following day was clear and warm, as in the early part of the breeding season. Several pairs investigated vines as if seeking nest sites, and several males were singing vigorously. It was at this time that nest eleven was begun. After several days this activity again declined. Sporadic interest in nest sites continued into June, but no new nests were found on the study area.

During the spring of 1959, heavy rains were over by April 1. Nesting was underway by April 9 and continued until early July. There were no breaks in nesting activity such as were observed in 1958, and song and activity of House Finches around nest sites continued for a longer period in 1959. The cessation of activity coincided with the onset of the foggy mornings which are characteristic of Berkeley summers. In 1959, the weather

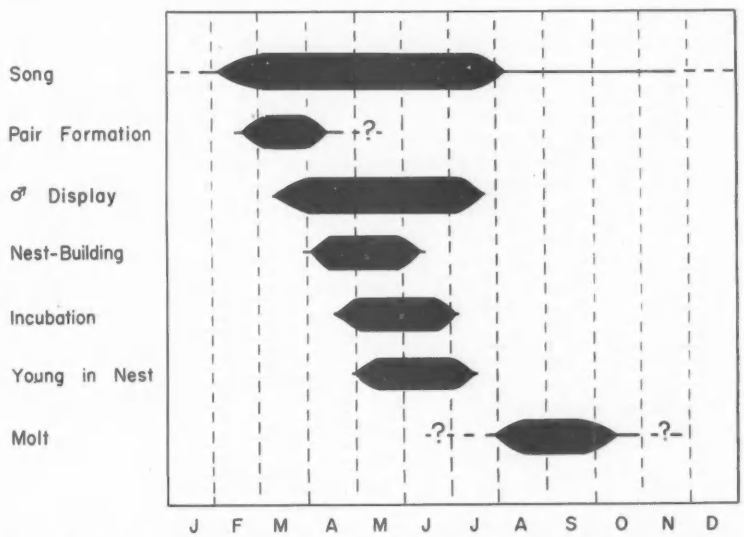

Fig. 1. Sequence of events in the annual cycle of House Finches in the San Francisco Bay area.

was unusually warm and clear during May, June, and early July. An explanation for the nesting calendar of 1958 therefore presents itself. Nesting began to wane in late May as a result of cool, foggy mornings during which song and breeding activity were noticeably decreased, and the second surge in breeding activity in June of 1958 may be explained as a result of a break in the series of cool, overcast mornings which inhibited nesting activities. The recurrence of foggy mornings a few days later terminated the breeding season in the study area.

The surge of breeding activity after the early April rains in 1958 may be interpreted as a result of delay imposed by the heavy precipitation. Photoperiodic influences may be supposed to have brought many of the birds into breeding condition before the end of the week of rainfall, but the unfavorable weather inhibited the building of nests. John Davis (personal communication) tells of having observed similar increase of nesting activity of Brown Towhees after heavy rains had prevented nest building. Observations of nest building in 1959 indicated that several pairs of House Finches began to build at about the same time but not with such synchrony as in 1958. The return of clear weather after the last heavy spring rain that year apparently served as a stimulus for several pairs to begin at about the same time.

PATTERNS OF AGGRESSIVE BEHAVIOR

The term "aggressive" refers strictly to attack, whereas the term "agonistic" includes escape, defense, and passivity, as it was defined by Scott and Frederickson (1951). Both terms will be used throughout the discussion in a fairly strict sense.

Supplanting attack.—The simplest and most direct form of hostile behavior is supplanting attack. One bird flies to the perch where a second is sitting, flying directly toward the second individual or to a point just beside it. The second bird usually flies or moves away before the aggressor alights. Occasionally the attacker is itself attacked by the perched bird, and violent combat usually follows. Marler (1956) describes how the attacking Chaffinch fixates its victim, calls, may tail-flip, and then flies to attack, but there is seldom any evidence of special behavior prior to supplanting attacks of House Finches. Likewise the victim shows no sign of fear or avoidance before moving, unless it has been chased or supplanted by the same individual just previously. Occasionally the sequence similar to that described for the Chaffinch may be observed in the House Finch in captivity, but it has been observed only rarely in the wild. Like the Chaffinch, House Finches show little sign of conflict in their behavior, either as aggressor or victim, and no displays result from supplanting attacks, except for the infrequent occasions on which the attacker misjudges its victim and is itself supplanted by the intended victim.

Often supplanting attacks occur without accompanying call notes, but occasionally the attacker will employ the *chit-chit* call characteristic of "head-forward" displays and attacks (table 2). Supplanting attacks occur most often at feeding places but may also take place at favorite perches, or in the territories established by breeding pairs in the spring. When the attack is made at a feeding place the primary incentive seems to be the food itself, rather than attacking the victim. In territorial defense, however, the intruder becomes the main incentive. Some birds appear to be unusually aggressive and interrupt feeding to supplant others several feet away.

As Marler (1956) and Hinde (1955–1956) suggest, a supplanting attack is often a more confident expression of hostility than any other form of aggressive behavior. The attacker does not hesitate to fly directly at another bird. If it does hesitate, it pauses in an intention movement of flight toward the opponent, which produces the display described below as the "head-forward" display.

Table 2

Summary of House Finch Postures and Associated Call Notes

Posture	Call notes	Circumstances in which given
Aggressive or avoidance		
Supplanting attack	"chit-chit," or "cheee"	At limited food source or favorable perch
Head-forward	"chit-chit," "cheee," or "tzeep"	At limited food source or favorable perch
Actual combat	"chit-chit," or "cheee"	Failure of "victim" to yield to attacker after head-forward display or supplanting attack
Beak-fencing	"chit-chit," or "cheee"	Failure of "victim" to yield to attacker after head-forward display or supplanting attack
Avoidance	none	When perched near a superior
Fear reaction	"zeet" (very soft)	When frightened by a loud noise or some other disturbance
Struggling to escape	"keeeeet," or "ahnn....."	When caught or held, or fighting while confined in a small space
Non-aggressive		
Begging by female or fledglings	"chee-chee-chee"	Young off nest, or female before and during incubation
Billing	twitter	Courtship, pair formation
Perching, legs extended	"keet," "coot," or "kweet" (interspersed with other call notes or given alone)	Curiosity, or mild alarm
Perching upright	"cheeup"	Mild alarm, isolation, location of companions. Sometimes given in chorus.
Courtship display, dance	song, with stressed "tzeep"	Courting strange female
Song flight display	song	Flying from one song post to another. Rarely used before supplanting another male.

Head-forward display.—A common form of hostile display between perched birds is the head-forward display (Hinde, 1955–1956; Dilger, 1956). Depending on the circumstances and the degree of hostile motivation, the display may take several forms. Two arbitrary positions in the gradient of postures from no hostility to extreme hostility will be described. These are referred to as (a) low intensity head-forward display and (b) high intensity head-forward display.

(a) Low intensity head-forward display. The body of the aggressor is slightly tipped toward the horizontal (see fig. 2A). The legs may be flexed slightly more than is usual when standing, the neck is stretched toward the bird about to be attacked, and the beak may or may not be opened. The wings usually remain in place partially covered by the contour feathers. The body feathers are usually sleeked, but occasionally, particularly if the attacker is a female, the breast, forehead, back, and upper belly feathers will be "shuffled," to use the term suggested by Moynihan and Hall, 1954 (see fig. 2B). The bird may hold this posture momentarily, then move toward the other individual if it has not moved away at the first sign of head-forward display.

Usually the low intensity head-forward display is accompanied by no vocalization. It occurs most frequently when a bird of lower rank comes too near a superior at a feeding place, or on a perch, violating the minimal limits of individual distance, an area around the individual which is free of all others. Individual distance, as described by Conder (1949), is a variable quantity in the House Finch, which changes according

to the "mood" of the bird and the circumstances. Birds may roost in contact with each other, although usually there is some space between them. In the daytime, however, the minimum individual distance observed in resting birds is about 15 centimeters. Individual distance of males increases during reproductive activity and when a male is near his

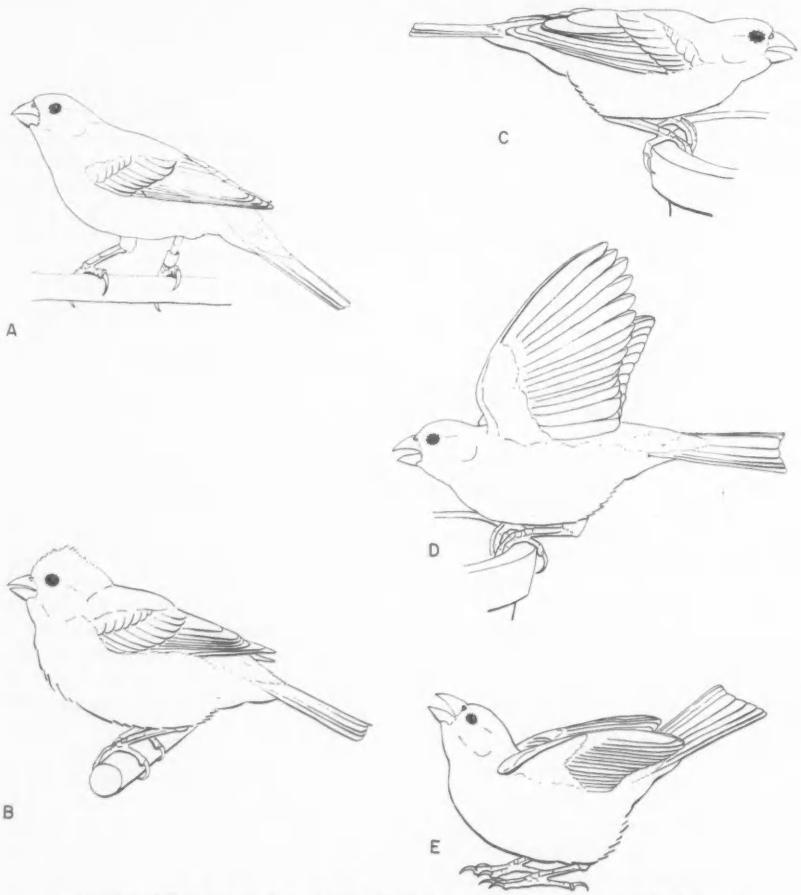

Fig. 2. A and B, forms of low intensity head-forward display; C, D, and E, forms of high intensity head-forward display.

mate he may supplant another bird that comes within 15 to 20 feet, or even more. Territorial behavior is extremely variable in any one individual from one time to another.

(b) High intensity head-forward display. The body of the aggressor is held in a horizontal position, the legs flexed to such a degree that the tarsometatarsus is almost parallel to the axis of the body (see figs. 2C and 4B), the neck is stretched forward along the main axis of the body, and the beak may or may not be opened, but it is not snapped.

Usually the beak is opened at higher levels of aggressive motivation. The wings are usually held folded over the back in a normal resting position, partly covered at the wrist. Body and head feathers are usually sleeked, although rarely the shuffling feather posture may be used, as with low intensity head-forward displays. Tail, body, neck, and head form a straight line pointing at the bird which is being attacked. If the bird being attacked is above the attacker, the straight-line posture is changed, so that the head is pointed toward the second individual (see fig. 2E). When the head is raised, the tail feathers also may be raised slightly above the usual horizontal position. If the second bird does not yield at once, or if it offers a counterattack, the first usually lunges forward, either supplanting the other, or engaging in combat with it. Marler (1956) suggests that head-forward display as it occurs in the Chaffinch is associated with a conflict of some sort. As in the Chaffinch the most extreme form of House Finch hostile display occurs in the high intensity display and is apparently associated with conflicting motivation (see following). This display usually occurs at feeding stations or in cages where the individual distance may be violated.

A loud, harsh *chit* call is given during aggressive display. It appears to be a very abbreviated form of the customary flocking call. One female used a harsh *tzeep* or *tzeet* call when attacking other birds.

The most intense form of head-forward display is sometimes accompanied by a complete or partial extension of one or both wings (see fig. 2D and 4D). The wings may be fully or only partially extended. The wing is rotated at the shoulder and extended at both elbow and wrist, or only at the elbow. Sometimes the wings are just lifted from the supporting contour feathers and held in a horizontal plane, still folded. This is accomplished by rotating the wing at the shoulder but not extending the elbow or wrist. Wing raising is a flight intention movement commonly associated with high intensity head-forward displays (Hinde, 1955–1956; Marler, 1956).

Combat.—If a bird which is supplanted or which is attacked by another in head-forward display resists the attacker, actual combat may result, or the attacker may yield at once and move away. Usually combat consists in the pair's hovering in mid-air, loudly and rapidly calling *chit-chit-chit*, each pecking vigorously at the other's beak, and grappling at the opponent with the claws (see fig. 3C). Sometimes combat between males leads to vigorous singing by the winner or by both combatants after they separate.

A less violent form of combat is "beak-fencing," which is less common than the struggles just described. It is much like the "billing" which occurs during the early part of pair formation, but it is much more vigorous, and usually occurs between birds of the same sex. It, too, is usually accompanied by loud calling consisting of a sharp *chip* note given in variable series.

Physical combat is of relatively rare occurrence between House Finches, but it sometimes occurs in the early stages of a change in hierarchical status among caged birds, or in dispute at feeding stations among wild birds. It is of short duration when it does occur, and no serious injury seems to result.

Billing is a gentle pecking by a male at the bill of a female. It appears to play some part in the establishment of a pair bond. It gradually evolves into courtship feeding as the pair bond becomes stronger. The details of this transformation have been described earlier.

Avoidance.—There is no certain posture associated with avoidance behavior—one bird simply moves out of the way of another which is attacking or supplanting it. There appears to be no raising of feathers along a large part of the dorsal and ventral tracts as Marler (1956) describes for the Chaffinch, and there is very little evidence of the "shifty" gaze which the Chaffinch displays. Birds which are subordinate in the hierarchy

tend to stay out of the way of dominant individuals. If it eats at a feeding tray near a superior, a bird will pick up bits of food with quick lunges at the food source, withdrawing its head to eat, and often leaning or facing slightly away from the superior. Often a given individual will stay away from food or water, only just a few inches away, in order to avoid a superior. It is often possible to obtain a good estimate of a hierarchy

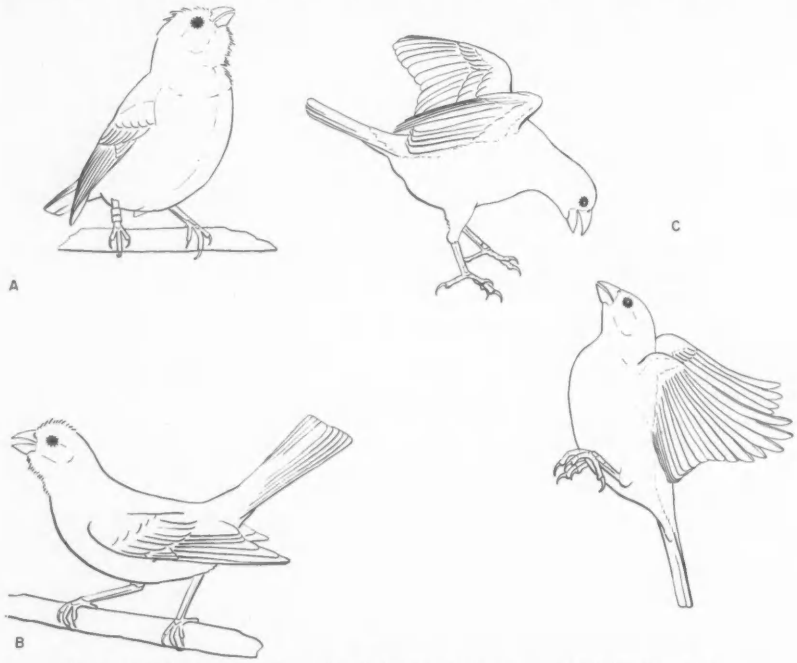

Fig. 3. A, typical song posture of male House Finch; B, "courtship" display posture of male House Finch; C, combat between two House Finches.

by noting the avoidance of certain birds by others, as well as the pecking or supplanting of some by others. Avoidance behavior is noted most often at feeding places or at water, wherever birds gather together. Marler has noted (1955) that avoidance behavior tends to be discarded during a period of severe hunger. A bird will endure much more abuse from a superior if starved.

As would be expected from a bird trying to remain inconspicuous and out of the way of another, no calls are associated with avoidance behavior.

Fright response.—The most frequently observed fright response in the House Finch is flight from wherever the bird was disturbed to an elevated perch nearby if the fright was mild, or to some distant place if the fright was severe. Occasionally a bird will crouch, with body noticeably tensed, neck extended slightly so that the head points forward in line with the body axis, and feathers sleeked. The posture is almost identical with the posture of an intense head-forward display. It is so little ritualized that it should be properly called a flight intention movement rather than a formalized display posture as is the head-forward display. Both postures have undoubtedly developed from

the same motor activity—flight takeoff—but are released by different stimuli. The fright reaction is often accompanied by a very soft *zeet*, sometimes given by only one of a group of birds.

Another possible expression of mild fright is an extension of both legs and the neck, so that the bird assumes a stiff-legged, erect posture (fig. 4A). This is a silent reaction which usually gives way to a more relaxed position and the usual conversational call notes, or to flight.

If a bird is caught and held in the hand it often utters a loud and nasal-sounding *ahnn-n* while it struggles to escape. Sometimes when several birds are confined in a small container they will fight, and one, apparently the loser, will utter this same sound.

Conflicting motivation.—Head-forward display is often accompanied by ruffling of the feathers of one or more parts of the plumage. Hinde (1955–1956) and Marler (1956) suggested that for other passerine birds this denotes a conflict in motivation, often between attacking and fleeing. The most vigorous head-forward displays of the House Finch are given in circumstances which suggest that there is some such conflict whenever the head-forward display is given instead of a direct supplanting attack. The forehead feathers are the ones most often ruffled when there is conflict between fleeing and attacking or feeding, or other tendencies. At times, however, the feathers over most of the body may be ruffled. It has been mentioned that attacking females sometimes ruffle during head-forward display (see fig. 2B). A caged, incubating female had occasion to chase intruders from the edge of her nest several times. Here the conflict might be between incubating and attacking. Other birds of both sexes which have ruffled plumage while in head-forward display might have had conflicting fleeing and attacking tendencies.

The forehead feathers alone may be shuffled while a bird is feeding near an observation window where the observer is partly visible. Here the conflict would be between eating and fleeing. In the sexual display of the male the forehead and throat feathers are shuffled, and the rest of the display probably involves a conflict between fleeing and sexual tendencies, but these same feather tracts are also shuffled when the male sings by himself with no apparent cause for conflicts between either hostile, sexual, or fleeing tendencies. The motivation of this feather posture is undoubtedly related to the motivation of song, which at the present time is a much debated, but little understood phenomenon. Full House Finch song, whatever its motivation, does involve a considerable expenditure of energy and emotion, and this may involve sympathetic "pilomotor" activity as Morris (1956) describes.

Likewise, wing extension appears to be associated with conflict. Hinde (1955–1956) suggests that it is an expression of extreme hostility, and it does occur in the House Finch in circumstances which involve extreme hostility, but still there must be some element of fear, or tendency to flee, else the bird would attack without display, as is customary in the relationship of a high-ranking individual toward one lower in the hierarchy. If there were not some conflict, the intention movement of flight (wing raising and extension) would immediately be completed as an actual flight toward the opponent.

Head-forward displays are most often given toward strangers of the same or different species, or after long continued supplanting of members of a known group. In either case there is probably a conflict between attack and some other tendency—in the first, perhaps an uncertainty as to the aggressiveness of the opponent and fear to press an attack too fast; and in the second, increasing weariness and a desire to rest.

SONG

For the House Finch, song does not appear to have the strong connection with territory which it has for the European Robin, *Erithacus rubecula* (Lack, 1943) or the Song

Sparrow (Nice, 1943). Several males may perch in one tree, some preening, some chirping, and some singing loudly. In cages one bird may sing loudly for several minutes without receiving any special attention from his superiors in the flock hierarchy. At other times, however, a singing captive male may be chased by his superiors. House Finches were never seen to engage in song duels at the territorial boundaries such as are described for other species by Nice (*op. cit.*) and Lack (*op. cit.*). Usually, however, singing

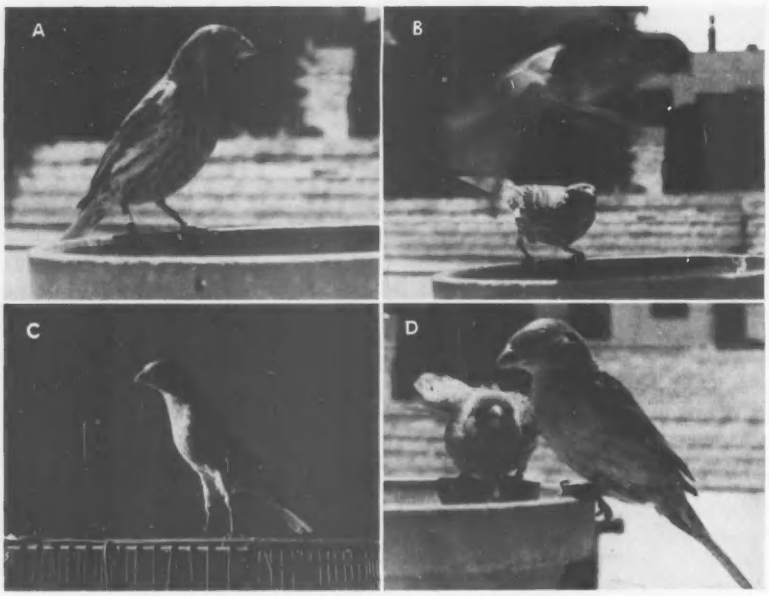

Fig. 4. A, stiff-legged erest posture of mild fright; C, stiff-legged erect posture of extreme fright; B and D, two forms of high intensity head-forward display. In D the female House Finch on the left is displaying toward a female House Sparrow.

individuals are spaced at greater intervals than individuals which are not singing. Males may sing as close together as 25 feet apart without interference, but one often supplants the other if they are closer to each other. Likewise, if two birds are singing simultaneously in a cage, one usually supplants the other.

The song of the House Finch may be described as a rambling warble, ending, when given with full intensity during the breeding season, with a final *tzeep*. This end syllable is given with a rising inflection. A sonogram of a characteristic House Finch song is illustrated in figure 5.

After a period of silence lasting several weeks during the molt, from about the end of July through the middle of September or the early part of October, relatively weak and incomplete song is heard irregularly from adult males. From then on it wanes but does not cease entirely. During most of the winter sporadic singing, usually by single males, may be heard during the day. It is heard more commonly on the lower campus of the University of California than in residential areas of Berkeley, although House Finches are still present in the residential areas. The song given at this time is less

vigorous than that of the breeding season and lacks the ending *tzeep* which is characteristic of spring song.

In the San Francisco Bay area House Finch singing begins to increase in early February. In residential areas the birds may group together in flocks, singing, preening, and feeding. During this period, song may be very loud and vigorous. The bird flies from perch to perch, almost as if claiming a territory, but no hostility is evident between individuals. A male may sing from a tree in which several other males are resting, without showing any aggressive inclinations toward them and without evoking any overtly hostile responses from them.

A male singing with full intensity stands in a posture characteristic of many passerines. Usually the tail is raised just above the line of the body axis, the head is tilted slightly and the beak is opened, sometimes partly opening and closing rapidly with the rhythm of the song. The wings usually are held in place under the body feathers

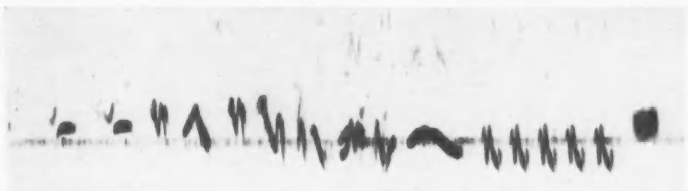

Fig. 5. Sonagram of complete adult male House Finch song, recorded by P. R. Marler. Duration, 2.1 seconds; frequency extremes, about 2000 and 5000 cycles per second.

(see fig. 3B) but rarely may be slightly drooped. The feathers of the chin and forehead are ruffled. Often the bird turns slightly from side to side with the rhythm of the song. Winter song and much of the singing done during the breeding season are given with lower intensity, lacking the final *tzeep*, and usually are shorter and softer than song of full intensity. When singing this "incomplete" song the bird usually perches with legs flexed in a normal perching posture, or it may be squatting on a perch resting the body on the feet, with feathers slightly fluffed. This posture is often observed in birds singing during mid-afternoon.

Females, too, may sing the "incomplete" song, most often during March and April. A hand-reared female kept indoors and exposed to a rather irregular schedule of illumination sang often during November and December. One captive female was repeatedly observed to sing softly, sitting on one foot, with her eyes closed. Female song has been observed in several different situations in the wild. In caged birds it was noted most often while the bird was resting. Wild females have been observed to sing both while alone and in the company of the mate, but in either situation it is of rare occurrence.

Males frequently sing or call while flying. A bird may fly long distances between song perches, giving a burst of song just after taking off. During such long flights the song may give place to the *cheep* call. When males are released after being banded or trapped, they often sing loudly during the flight from the trapping station. On several occasions females were observed to sing upon release.

Occasionally "song-flight" displays are performed by male House Finches. Usually these are short flights from one prominent elevated perch to another. The bird flies slowly with a "butterfly flight" such as is described by Conder (1948) for Goldfinches, Hinde (1955–1956) for canaries, and Marler (1956) for Chaffinches. The wings appear to be held more rigidly than usual and do not seem to make a complete downstroke. For the last 20 feet or so the bird glides with wings spread and held slightly above the hori-

zontal, still singing vigorously. Song flight has been noted early in the spring, before many birds were associating in pairs, and in June after the first broods had left the study area. The display appears to be performed most often, if not exclusively, by unpaired males. It is not associated with aggressive activity toward other males, as is the song flight of the Snow Bunting (Tinbergen, 1939), although on one occasion a male was seen to use this display when supplanting another male.

Marler (1956) describes a "whirring flight" used by Chaffinches when flying in very dim light or darkness. This type of flight is also used by House Finches under similar circumstances, as when they are disturbed at the roost.

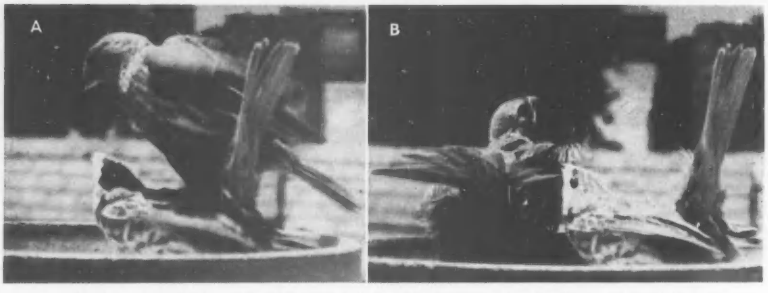

Fig. 6. A, copulation of male House Finch with dummy female; B, postcopulatory display of male House Finch beside dummy female.

COPULATION AND SEXUAL DISPLAY

Copulation itself does not appear to involve conspicuously overt elements of aggressiveness. The male House Finch, however, performs a display toward the female which evokes a hostile reaction from her, and since this display appears to be related to copulation, behavior leading up to and including copulation will be considered here.

Copulation normally occurs at the invitation of the female. Typically she pauses on a perch several feet from the nest, before entering with nesting material which she carries in her beak. The male is usually on another perch several feet away from her. She raises her tail to a vertical position, droops the wings and vibrates them as in courtship feeding, and retracts the neck slightly, at the same time tilting the head back, so that the beak points upward. The male may not notice her at once, and if he does not within a few seconds, she may resume a regular perching posture, fluff, shake, and proceed to carry her materials to the nest, or she may fly to another branch and repeat the invitation. If the male does see her, and he usually does, he flies to her at once, hops onto her back, his abdominal feathers fluffed, flaps his wings to maintain his balance, leans back, his tail pressed against the underside of hers, and apposes his cloaca to hers (fig. 6A). When he hops off or falls off, both birds may resume a regular perching position, fluff, and shake. The female then usually goes onto the nest. Frequently, however, the male, as soon as he hops off the female's back, especially if the copulation has been complete, assumes the same crouching posture as the begging female or juvenile—legs flexed, body held horizontal, feathers fluffed, tail slightly raised, and wings drooped and fluttered, head held back, but slightly up, uttering a soft twittering (fig. 6B). On two occasions the female then mounted and went through the motions of copulation, lowering her tail, flapping her wings to maintain balance, and touching the male cloaca with her own. After copulation both birds fluff their feathers and shake. The male may then preen, while the female flies to the nest to work into it the material she still carries in her beak.

Twice a male was seen to attempt copulation with a strange female which was preening and shaking her feathers. She was pulling her primaries and breast feathers alternately, shaking her body with tail held up, and wings fluttering, as in bathing. The male, whose mate was incubating, approached her with his neck stretched up as if about to mount, but she supplanted him. The male stood watching the female, which resumed her preening, again shaking with raised tail and fluttering wings. The male again approached her with head up, and legs extended stiffly as if to mount, but again she supplanted him and this time flew to another perch.

During the breeding season the male House Finch performs a display which does not appear to be involved in pair formation and which does not usually lead to copulation, but which does seem to have some sexual motivation. The male stretches his neck up and slightly back, with head tilted slightly upward, body feathers usually rather sleek, but forehead and chin feathers ruffled, wings slightly drooped, and tail raised to a vertical position slightly spread. The legs are usually flexed, thus placing the body in a horizontal position. The bird hops toward a female, turning slowly from side to side (pivoting), singing very loudly, and emphasizing the ending *tzeep* phrase. Sometimes several *tzeep* phrases are inserted between repetitions of the complete song. Usually this display is directed by the male to a female other than his mate. Although it does occur before the first nesting of the season, it appears most often and in its most intense form well along in the breeding season after most birds are paired, and so does not seem to be a common method of pair formation. The female as a rule repeatedly supplants the male when he comes within two feet or so of her, and if her mate is in the vicinity he usually supplants and chases away the displaying bird. Sometimes the noise attracts other males and the female may chase off several different males, each displaying to her one at a time. The female usually flies some distance away under these circumstances and is usually not followed by more than one male, if by any.

On one occasion a female did not supplant a male which was displaying toward her, and he approached to within six inches of her. When she neither supplanted nor solicited him he stopped his display and perched quietly beside her.

The display is apparently part of pairing and mating, as is demonstrated by the use of a stuffed female mounted in the invitation posture. Near the end of the breeding season in July, 1958, a stuffed female was placed at a feeding station frequented by House Finches. A male soon flew down to eat, landing two feet from the food tray on which the dummy was standing. He looked at the dummy for a few seconds, then hopped toward it. He stopped momentarily beside it, stretched his neck up, fluffed his belly feathers, dropped his wings slightly, and hopped onto the dummy, carrying out the complete copulatory act. Then he hopped down and crouched beside the dummy, twittering, as described above for reverse copulation. His abdominal feathers were still fluffed, the wings drooped, tail spread and raised, and he leaned away from the dummy, almost lying on his right side. He continued this for almost a minute, then stood up and began to display before the female dummy. He circled around it, going from the right side to the front, to the left side, and then hopped onto her back again. This time he stood with head and neck erect, belly feathers fluffed, tail spread and lowered, as before, but spent more time placing his cloaca in contact with that of the female. In so doing he caused the tail of the dummy to fall into a horizontal position. When he hopped down he stood looking at the female, still twittering, tail erect, body feathers slightly fluffed, but not crouching as before. After pecking at seed on the ground and chirping softly, looking at the dummy from time to time for several minutes, he began to sing and display again, but not so vigorously as before. He again hopped onto the dummy whose tail was still in a horizontal position, and attempted copulation, then jumped off and began to feed.

Daanje (1941) described a communal display of the House Sparrow in which several males, including the mate, may display before a female which is not in reproductive condition. Summers-Smith (1954) maintains that this display is not simply a nonfunctional performance retained from some time in the past history of the species when it had a functional significance in courtship, but that it still functions as a stimulus to the female, leading to reproductive synchronization of the two sexes. Daanje suggests that the display originated as an attempt by the male to induce the female to copulate. Armstrong (1947) and Darling (1938) have described the function of display in birds generally as bringing the individuals involved into reproductive rapport.

Perhaps the display of the male House Finch also originally had this function, but, as in the House Sparrow, it no longer occurs regularly in this connection, except in unusual circumstances such as the one just mentioned involving the dummy. We may ask why the sexual displays of males of both the House Finch and the House Sparrow have lost their supposed earlier function as a precopulatory display occurring at the onset of the breeding season as well as later. As Summers-Smith points out, the display is highly stimulating to males and attracts them from all around. The same is true with male House Finches. The sound of a male displaying to a female attracts males from some distance away. In a cage containing several pairs of House Finches, attempts at copulation are always unsuccessful because the male attempting copulation is always knocked off the female by the other males. A conspicuous precopulatory display in such a semicolonial species as either House Finch or House Sparrow would, then, be very dysgenic, and successful copulations in both species usually occur after a postural invitation by the female. The female House Sparrow employs the juvenal summoning call which probably is not sexually stimulating to other males in the vicinity, but it attracts the attention of her mate. The female House Finch assumes a silent soliciting posture. Copulation then usually proceeds without interference from neighbors.

From the evidence at hand it appears that the display may serve more to induce a second nesting than a first attempt, or especially to induce a second if the first attempt fails, since the display occurs most often near the end of the first nesting period. In view of the very limited number of second broods observed in the study area this stimulation of the female, when successful, may be very important to the species. It is not clear why the display does not occur more often early in the season before the first nest building. A possible factor is failure of the reproductive drive of the male to reach the threshold necessary to release the display at this time of pair formation. Experiments with a dummy female in soliciting posture indicate that the male can be induced to display only when the gonads are enlarged during the breeding season. It is possible that the almost constant contact with the female, involving billing and courtship feeding, provides an outlet for the sexual motivation building up before nest construction begins. Only after the female mate begins incubation is the sex drive thwarted, and the males may display toward any strange female they encounter. The display of the House Finch appears to be associated, then, with a strong and thwarted sexual motivation which, however, may lead to continued breeding effort, as discussed above. When the female does not permit the male to come near her, he performs the display toward her.

The pivoting of the male House Finch during his display probably involves the same alternate flying-toward and flying-away tendencies as the pivoting of other fringillid species (Hinde, 1955–1956). It seems likely that this hesitation in the approach of the male toward a strange female is related to the general dominance of the female over the males. Probably the display is not usually performed toward the mate because the male is accustomed to approaching close to her, and the conflict of approach and retreat tendencies does not occur.

SUMMARY

The agonistic behavior of the House Finch is described with an emphasis on aggression and dominance relations. Part I of this paper is concerned with annual cycle and display patterns. Both wild and captive birds were observed intensively in central coastal California, chiefly in Berkeley, in 1954–55 and in 1957–59.

Loose aggregations of House Finches may be observed in rural and suburban areas during the winter. In the Berkeley area, males become established on their breeding areas and begin to sing in late February and early March, and about this time pair formation takes place. Nesting begins in April and may continue into early June. After the young leave the nest and become independent, both adults and juveniles tend to aggregate in large groups where food is plentiful.

During early spring when pairs are forming, the aggressive behavior of wild birds reaches a peak. Males defend the area around a female, as well as a space around the nest, but there seem to be no well-defined territorial boundaries which are strongly defended. The average size of the territories observed was 642 square feet.

The simplest form of hostile behavior observed in House Finches is supplanting attack. Another common form of hostile display between perched birds is the head-forward display, which may be of either low or high intensity. Hostile displays may give way to actual combat, which may be a vigorous struggle or merely beak-fencing, or billing. Subordinate individuals avoid those above them in peck order; fright responses may by either immediate flight, crouching, or a stiff-legged, erect posture.

Ruffling of the feathers of one or more parts of the plumage, or extension of one or both wings may be associated with a conflict in motivation.

Copulation in the House Finch normally occurs at the invitation of the female. Occasionally reverse copulation occurs. The male performs a striking, sexually motivated display toward females and this may serve to bring the sexes into reproductive rapport.

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SONG VARIATION IN A POPULATION OF BROWN TOWHEES

By PETER MARLER and DONALD ISAAC

With the advent of new methods of analysis, the study of variation in bird song can be approached with more objectivity than has hitherto been possible. As with morphological characters, careful study of variation may throw some light on the kind of selective influences to which vocal signals and other communicatory behavior are subject. The problem of describing variation in behavior is confounded by the extensive variation which we sometimes find within the same population and even within the same individual at different times.

In a previous paper (Marler and Isaac, 1960) we have given a preliminary description of the situation in a simple case, the song of the Chipping Sparrow (*Spizella passerina*), in which variation within the individual is minimal. The singing of the Brown Towhee (*Pipilo fuscus*) is somewhat more complex and it is our intention in this paper to establish the limits of variation in the songs of the individual and in a sample of a number of individuals from the same geographical area.

ACKNOWLEDGMENTS

The authors are greatly indebted to John Davis for discussing the problems raised in this paper and for giving the benefit of his familiarity with towhees in his criticisms of the manuscript. The recording expedition to México was made possible by a grant from the Associates in Tropical Biogeography of the University of California. The analysis of the songs was carried out under the auspices of a grant from the National Science Foundation.

METHODS

The methods of recording and physical analysis are the same as those described previously for the Chipping Sparrow (Marler and Isaac, *op. cit.*). Once again three types of analyses are presented, all made with a Kay Electric Company Sonagraph. Most of the data come from frequency/time sonagrams, using the wide band-pass setting, and amplitude/time analyses were also made of some songs. The results of frequency/amplitude serial sectioning of single syllables will be published separately.

The field recordings were made between July 11 and 23, 1958, all within the small state of Aguascalientes in west-central México. The majority, 55 song types from 31 birds, were made within a 10-mile radius of Calvillo. The remainder, 6 song types from 6 birds, were recorded in the neighborhood of Rincon de Roma, about 40 miles from Calvillo. Most of the recordings comprise only a few selected songs from each bird, and these two samples are in general grouped together for analysis. An additional series of 53 songs was recorded from one individual on July 20, 10 miles west of Calvillo and is referred to as Calvillo B24. Songs of this bird are analyzed separately and are excluded from the analyses of the general sample. Two of the songs were recorded at slow speed and are excluded from the detailed analyses. Variability figures, unless otherwise specified, are given as the arithmetic means plus or minus one standard deviation.

SONG

General description of the song pattern.—A typical song of the Brown Towhees in the study area consists of two basic parts. First, a single soft introductory *chip*, then a pause, and then a louder, regular trill of some 5–20 syllables, lasting about 1.5 seconds (see fig. 1 A–D). The introductory syllable was not seen on some sonagrams. In the general sample, 40 had introductory syllables and 21 did not. Upon rechecking the re-

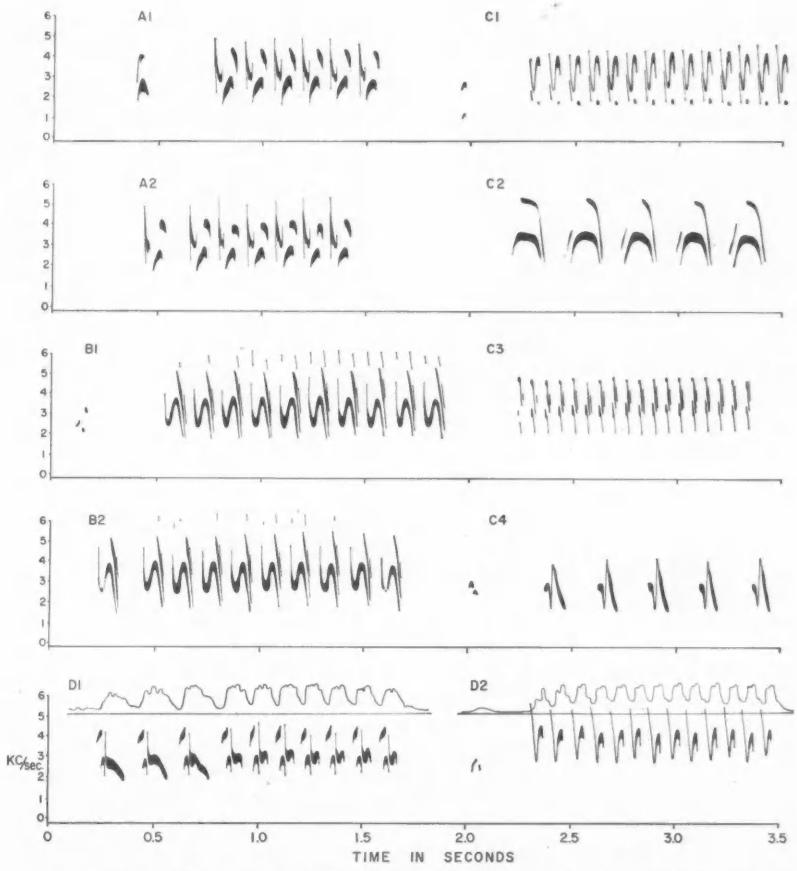

Fig. 1. Frequency/time sonagrams of ten songs of the Brown Towhee. These records can be read from left to right in much the same way as a musical score. A1 and A2, B1 and B2 illustrate the alternative methods of starting a song either with a special introductory note, or by one of the trill syllables which is displaced in front of the main part of the trill. C1 to C4 are songs from different individuals, emphasizing the variability in the number of trill syllables as compared with song duration. D1 and D2 also include some typical patterns of loudness or, more strictly, of amplitude modulation. Note how the soft introductory note in D2 is represented by a small deflection of the curve, while the trill syllables have a stronger effect.

cordings, it was found that four of the 21 had soft introductory syllables. Of the remaining 17, 10 had an alternative pattern. Instead of the introductory *chip* syllable, one of the trill syllables was displaced into the corresponding position. These two methods of achieving an introduction also occur in alternative renderings of the same theme (fig. 1, A,B).

In addition each bird possesses several distinct song types, identifiable by the dif-

ferent syllable structure. Figure 2 shows how five syllable types were used in 53 songs by Calvillo B24. Note how trills sometimes include two syllable types. This is particularly common when there is a change-over from one song type to another, the transitional song being half of one type and half of another (for example, song number 13 in fig. 2). Double trills apparently can also occur as distinct themes. Songs 26 to 47 in figure 2 all include both type C and D syllables. However, these double trills were rare in the general sample, accounting for only five of the 61 types recorded.

The temporal pattern of singing.—Brown Towhees in Aguascalientes normally select singing posts 20 to 30 feet above the ground and usually remain stationary while performing. In B24 the song duration was 1.49±0.19 seconds and the interval between songs was 11.6±5.4 seconds (fig. 3, A, B). Thus about 12 per cent of performance time was spent in song. Song duration in B24 was almost the same as in the general sample, the value for the latter being 1.52±0.31 seconds. Although song duration varies somewhat, variation in the number of syllables which make up the song is much more striking (fig. 3, C). The extremes of the general sample are 4 and 26, with an average and standard deviation of 10.4±4.5. For Calvillo B24 the corresponding values are 6 to 16 and 10.2±2.1.

The question then arises how variation in the number of syllables is related to song duration. Does a small number of syllables imply a short song? As can be seen from figure 4,A this is by no means necessarily the case. Although there is a trend for longer songs to have more syllables, a song with four or five syllables can be as long as one with 15. Thus the rate of syllable production varies widely, being 7.4±2.1 syllables/second in the general sample. This suggests the possibility that syllable duration may vary in an inverse fashion with the number of syllables per song. As figure 4,B shows, such a relationship does exist. In other words, a song may be made up of a few long syllables or of a large number of short syllables. The average syllable duration for the general sample is 101±57 milliseconds, and for B24, 116±25 milliseconds.

Frequency characteristics.—The variation in syllable structure, described later in more detail, results in wide variation in the pitch or frequency characteristics of the song (fig. 5). Among the 51 songs of B24 the maximum frequency ranges from 4.5 to 7.6 kilocycles per second, and varies even more widely in the general sample. Averages and standard deviations are 5.86±0.86 KC/sec. for the general sample and 6.50±0.71 KC/sec. for B24. Minimum frequencies vary somewhat less (1.84±0.35 KC/sec. for the general sample and 2.04±0.47 for B24). The frequency spread, however, differs remarkably from bird to bird, from as little as 2.0 KC/sec. to as much as 5.8 KC/sec. Once again the variation in B24 (4.47±0.73 KC/sec.) is only slightly less than that in the rest of the sample (4.01±0.92 KC/sec.).

Some of this variation in frequency is probably the result of amplitude variations, as has already been described for the Chipping Sparrow. In that species, syllable structure varies relatively little. In the Brown Towhee the greater degree of variation in syllable structure has a more dominant effect on frequency variation, and detailed measurements of amplitude characteristics have therefore not been made. A typical amplitude record is presented in figure 1,D, showing the weak introductory note and the approximately constant amplitude peaks of each syllable type in the trill.

Syllable structure.—The introductory syllable with which most songs begin is so soft that there are only a few good sonagrams. The best are shown as tracings in figure 6. All are considerably shorter than the trill syllables (42±17 msec. in B24, and 41±17 msec. in the general sample). The commonest pattern is a syllable with two or more frequency bands that first rise and then fall. Sometimes there are modulations on this

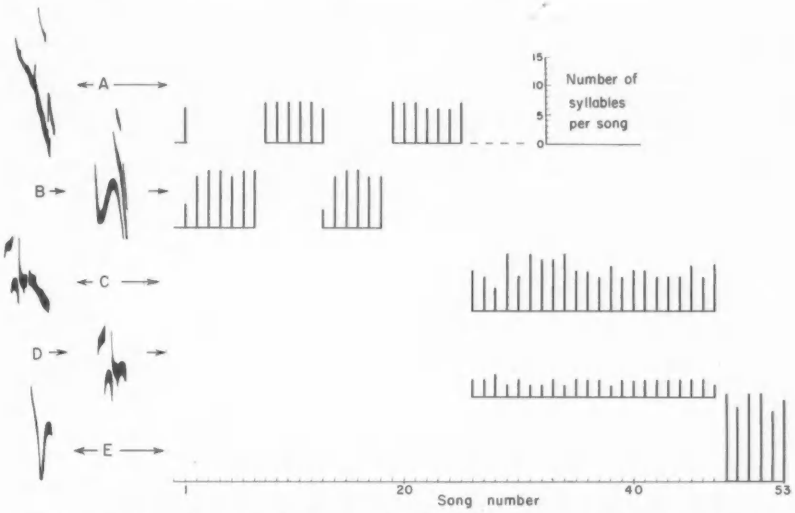

Fig. 2. A diagram of 53 consecutive songs of Calvillo bird 24. The syllable types are illustrated on the left. Their occurrence and number in a given song are indicated by a vertical line placed opposite the appropriate syllable and above the number of the song. Note how some songs include two syllable types and that types C and D always occur together. The number per song varies with different syllable types, being greater with short syllables, such as E, than with longer ones, such as B.

basic pattern, as in syllable E1 of figure 6. A bird may use an introductory syllable of a different structure with each different trill type (as in syllables J1–J3 of figure 6). Usually there is no apparent similarity between the structure of the introductory syllable and of the trill syllables with which it is used, but occasionally some resemblance is evident. Syllables C1 and J3 of figure 6 are reminiscent of their corresponding trill syllables (fig. 7:part I—syllable J1, and part II—syllable H3, respectively). The most striking case is figure 6: syllable N1, which is a miniature and slightly distorted version of the trill syllable (fig. 7: part IV—syllable E1). However, these resemblances are sufficiently uncommon that they may be a result of chance. As noted earlier the place of the introductory note is sometimes taken by one of the trill syllables which, apart from its spacing, differs in no way from those used in the trill.

A prime concern of this paper is the remarkable diversity of syllable types which make up the trill. Tracings of each of the syllable types found are shown in figure 7. They are arranged in four groups. Each of the first three include a sample of birds found so close together that we can assume they could hear each other. The diversity within a group is no less striking than that between groups. In many instances birds were actually recorded while countersinging. Yet no case was found of the sharing of a distinctive syllable type by two adjacent birds. The lowest line in figure 7 represents songs of birds from a number of areas. These are not obviously more diverse than those in the rest of the sample.

We may also note the variability in different syllable types of the same individual. The types used by B24 are shown in figure 2. Two of these syllables (C and D) are variations on the same pattern, but the rest are quite distinct from each other. The dif-

ferences between syllable types are rigidly maintained, with no transitions between them.

Similarly in the general sample we find examples from the same individual of syllable types which are different but related (see fig. 7: part I—syllables I1 and I2; part II—syllables B1, B2, and B3; part III—syllables D1, D2, F1, F2, and F3; and part IV—syllables B1, B3, C1, and C3). We also find syllable types in the same individual which are distinctly different (fig. 7: part I—syllables A1, A2, H1, H2, and H3; part III—syllables B1, B2, C1, and C2; part IV—syllables B2 and B3). At first sight it appears that some members of a group may share certain characteristics. Note, for example, the close resemblance of syllables C2 and H3 and of syllables D2 and E1 in

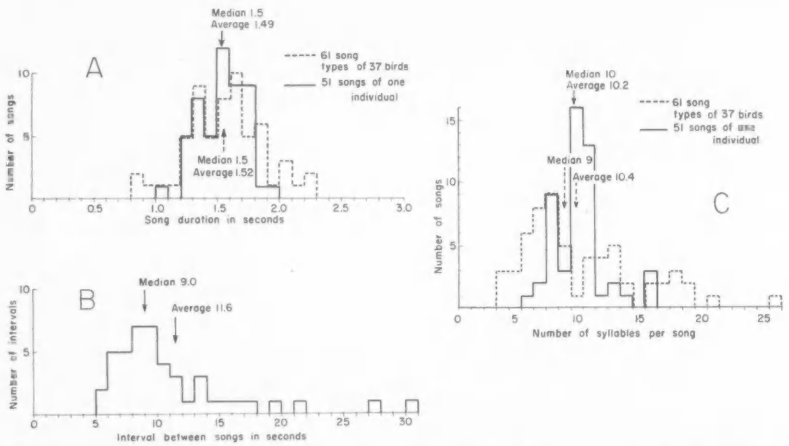

Fig. 3. Frequency distributions of (A) song duration in B24 and in the general sample, (B) intervals between songs in a bout of singing by B24, and (C) the number of syllables per song in B24 and in the general sample.

part I. However, comparable syllable types occur in different groups (see fig. 7: part II —syllable C1 and part IV—syllable K1; and also part III—syllable D2 and part IV—syllable F1). We must not overlook the possibility that comparison with a sample from a different area might bring out some subtle characteristics shared only by the members of this population. At the moment such shared characteristics of detailed syllable structure are not discernible.

DISCUSSION

The problem of describing song variation.—A description of the songs of a bird in a given area should include information on the characteristics both of individual repertoires and also of the song of the whole population. In the latter case it is clear that a large sample is necessary, but this need is not so obvious in describing the behavior of individuals. Where the song of the individual varies little, as in the Chipping Sparrow (Marler and Isaac, *op. cit.*) it is true that a small sample is adequate, but this simple condition is probably rare. The Brown Towhee is fairly conservative, in comparison with some of the more versatile songsters, yet a sample of 53 songs from one bird was hardly sufficient to define its repertoire. The histograms illustrating variation of song duration, frequency and number of syllables (figs. 3 and 5) in one individual are sur-

prisingly similar to those for the whole population. This may mean that the sample of songs from the population as a whole should have been larger for a truly adequate description. We are thus confronted with a difficult and time-consuming problem in describing variation in bird song, even with a species as conservative as the Brown Towhee. How much more serious this becomes with the more versatile songsters, such as the Song Sparrow, *Melospiza melodia* (Nice, 1943; Mulligan, MS) or, in Europe, the Robin (*Erithacus rubecula*), and the Mistle Thrush (*Turdus viscivorus*). One indi-

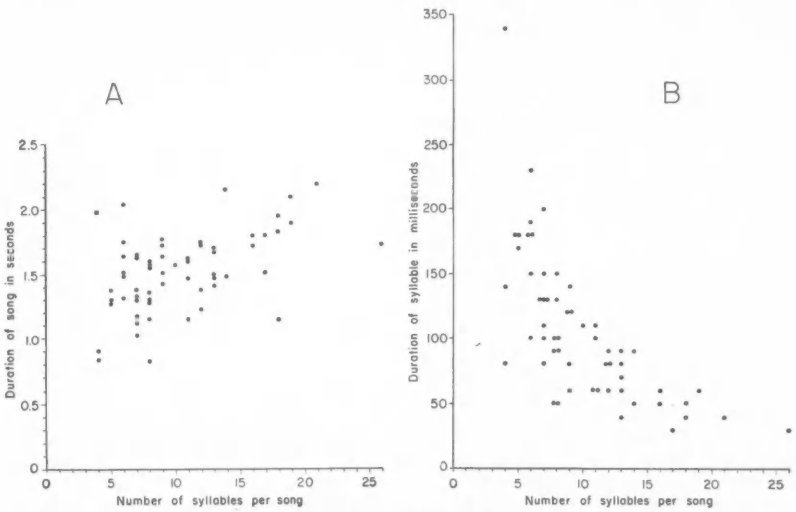

Fig. 4. (A) Song duration plotted against the number of syllables per song for the general sample. The trend for longer songs to have more syllables is present, but it is rather ill-defined. (B) Syllable duration plotted against the number of syllables per song. There is an obvious trend for shorter syllables to be repeated more often than longer ones.

vidual Song Thrush (*Turdus ericetorum*) gave 143 different songs in a series of 203, and the repertoire was still not exhausted (Marler, 1959). Characterization of the song of a population of such species is a major project, not to be undertaken lightly.

Song variation and continuity.—Hartshorne (1956) has suggested that variability in song is correlated with the continuity of singing, so that discontinuous singers are usually the least versatile. He cites many examples of a principle that holds in an appreciable number of cases. It remains to be shown whether this principle holds within a given family. Thus the Chipping Sparrow, which is a non-versatile singer, just qualifies as a discontinuous performer (by Hartshorne's criterion) with about 30 per cent of the performance period spent in song (Marler and Isaac, 1960). Brown Towhees are more versatile than Chipping Sparrows, yet one bird spent only 12 per cent of its performance period in song. Similarly, in the Rufous-sided Towhee (*Pipilo erythrophthalmus*), another variable singer, Davis (1958) finds that singing occupies only 9.1 per cent of the performance period. These may be extreme examples, but it seems that the concept of continuity will need to be re-examined when more data are available.

Song variation and recognition.—It has been argued elsewhere that the high degree

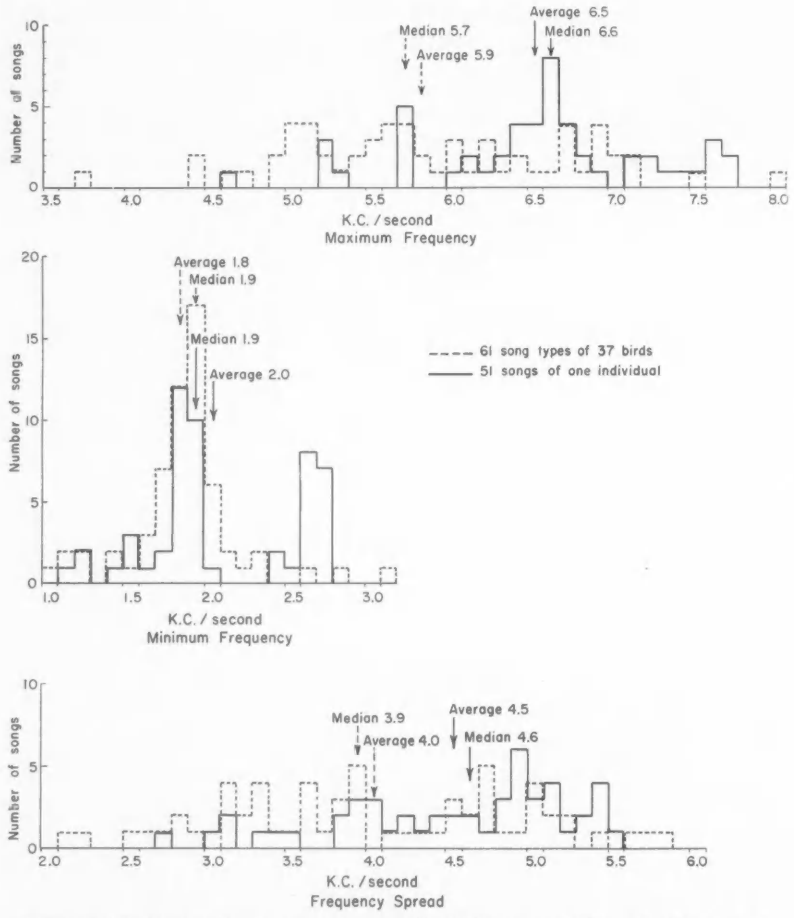

Fig. 5. Distributions of the frequency characteristics of the songs of B24 and of the general sample. Note the remarkable similarity in the two samples.

of variability which we find in the songs of certain birds is unlikely to be accidental (Marler, *in press*). There is evidence that some species use song both for species recognition and for individual recognition. These two functions are likely to encourage different evolutionary trends. To be effective for recognition purposes, a song needs to be distinctly different from other sounds likely to be heard at the same time and place. The most probable source of confusion in the sound background is the song of other birds. We would expect that the degree and kind of distinctiveness of the song of a given species should in some measure be related to the need for recognition.

The function of species recognition would seem to be best served by species-specific song which is stereotyped within a given population. On the other hand, the function of

individual recognition would require consistent individual differences in the songs of the members of a population. If both of these needs were present, natural selection would be encouraged to proceed in conflicting directions, favoring stereotypy on the one hand and variability on the other. There is reason to think that this conflict does in fact arise and is resolved in some cases by relegating the two functions to different variables of the song (Marler, *in press*). This hypothesis needs to be tested experimentally; but meanwhile, we can apply it to the songs of the Brown Towhee, to see which variables could serve the postulated functions of individual and species recognition.

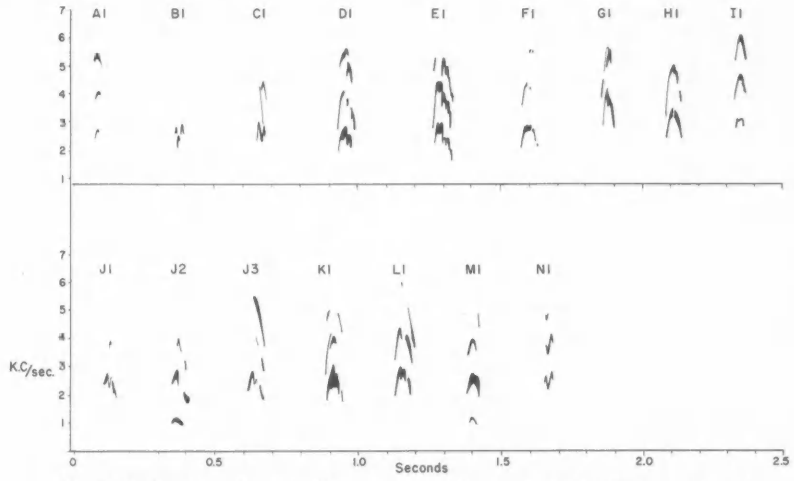

Fig. 6. Tracings from frequency/time sonagrams of some of the introductory notes of the songs of Brown Towhees.

The possible variables of songs of the Brown Towhees of Aguascalientes which we have described are: duration, temporal pattern, frequency pattern, syllable duration, rate of syllable production, and syllable frequency/time structure. Of these, the first two have relatively small variability and in particular the overall temporal pattern is strikingly consistent. Although more than one syllable type occasionally occurs in the trill, most songs consist of an introductory syllable followed by a trill of one syllable type. These characters might be used in species recognition. In contrast, the syllable characteristics are quite variable, especially frequency/time structure which is consistent in each syllable type of each individual and different between individuals, even when they are close neighbors. These could provide a suitable basis for individual recognition.

A comparison with the songs of the Rufous-sided Towhee.—The Brown Towhee ranges from southern Oregon in the United States to Oaxaca, México. The associated species assemblages and consequently the sound background vary considerably from one end of this range to the other. While songs of any species could influence the evolution of song characters, close relatives are particularly worthy of attention, where such relatives are sympatric. Confusion could exist because of similarities in vocalizations, general behavior, ecology and anatomy. Also the possibility of dysgenic hybridization may place a particularly high premium upon specific distinctiveness of characters in-

volved in reproductive isolation (Marler, 1957; Sibley, 1950). Information on songs of species similar to the Brown Towhee is sparse, but enough is available to speculate on the possibility of such interaction between the Brown and Rufous-sided towhees.

The range of the Rufous-sided Towhee includes most of that of the less widely distributed Brown Towhee. Recent studies suggest that these species may not be congeneric, *P. fuscus* being probably closer to the genus *Melozone* (Davis, 1951, *in litt.*; Sibley,

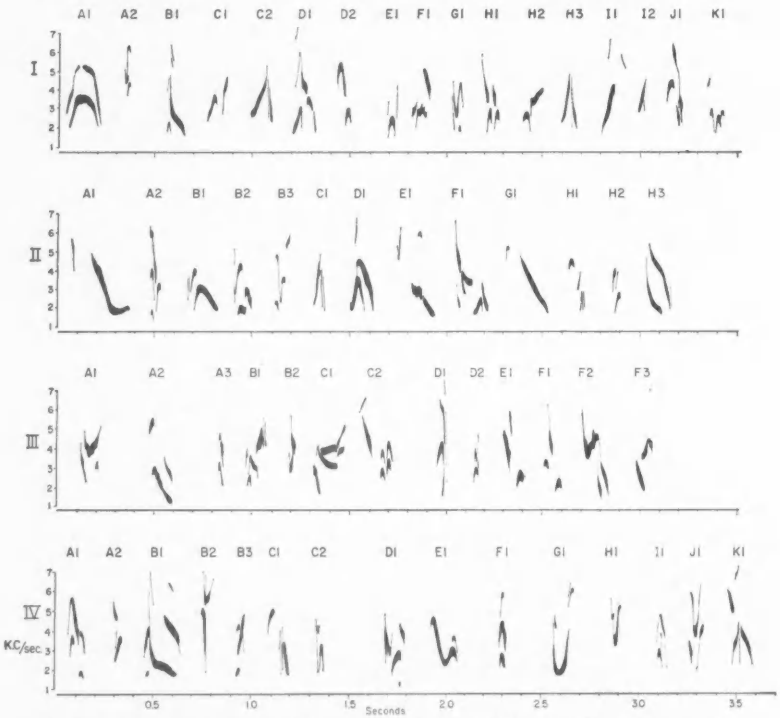

Fig. 7. Tracings from frequency/time sonagrams of 58 syllable types from the songs of 37 Brown Towhees. The three upper rows each represent a sample from a rather restricted area. The bottom row is a mixed sample from several locations. Alternative syllable types from the same individual are indicated by numbers, such as A1 or A2.

1955; Parkes, 1957). Thus it is probable that sterility barriers are well established between the two species, although it must be admitted that we do not know if hybrids can be produced in captivity. However, it is not necessary for them to be sibling species, in order to affect the evolution of each other's song. As long as they live together and are grossly similar in size and structure there is a chance that they may tend to produce similar sounds. If these sounds function in reproductive isolation a problem in achieving specific distinctiveness may thus arise.

The Brown and Rufous-sided towhees occupy different habitats in parts of their range, especially in México, but they cohabit closely in certain areas, occurring in the

same habitats in California, where they make frequent interspecific contacts (Miller, 1951; Davis, 1957). We may also note considerable resemblance between the structure of trill syllables in the Brown Towhee and the syllables in the terminal part of the songs of the Rufous-sided Towhee described from the eastern United States by Borror (1959), although the latter are somewhat shorter and are repeated fewer times, at a more rapid rate than in the Mexican Brown Towhees. The total duration of the songs of eastern *erythrophthalmus* and Mexican *fuscus* is also similar (about 1.3–1.5 seconds). It seems reasonable, therefore, to speculate on possible interaction between them in the evolution of their songs.

Comparison of the songs and singing habits of the two towhees in different parts of their range is hindered by the sparsity of information, but some attempt is possible. In the east, where *fuscus* is absent, *erythrophthalmus* has a considerably longer and more elaborate song than in California. There is a relatively long, complex and variable introduction, followed by a repetitive trill (Borror, 1959). In California there is a simple short trill, sometimes preceded by a single introductory syllable (Davis, 1957), and the trill seems to correspond with the terminal part of the eastern bird's song. The nature of the songs of *erythrophthalmus* in México is more difficult to ascertain, but they are probably closer to the eastern birds than to those in California (cf. Sibley, 1950). One bird recorded in Chihuahua used five basic song types among 24 songs. These consisted of a trill introduced by one or several syllables of various types, reminiscent of those described by Borror. The total duration (average, 1.4 seconds) was longer than that in California (0.4–0.6 seconds, Davis, 1957) and similar to that in the eastern states (1.3 seconds, estimated from some of Borror's data). We may also note from all populations of this species a striking degree of individual variation, involving more variables of the song than we have found in *fuscus*.

The songs of *fuscus* in México are probably not very different from those in California except that the latter have a change in tempo in the middle. A *chip* note is repeated three or four times, and then given in a rapid trill (Quaintance, 1938). Probably the same syllable type is used in both parts, thus corresponding with the alternative method of achieving an introduction used by the Mexican birds (cf. fig. 1) but with several repetitions of the introductory syllable. Double trills, with a change of syllable type partway through the song, evidently occur both in California and in México (Quaintance, *op. cit.*). There is, however, a radical difference in the seasonal pattern of singing in the two areas. In California, where the Brown Towhee is resident throughout the year and apparently mates for life, song is almost restricted to unmated males and as a result is seldom heard (Quaintance, 1938; Davis, 1957). In Aguascalientes there was persistent singing throughout the day from birds which were mated and breeding in July.

We can summarize the points which emerge from this comparison as follows:

1. In México, where *fuscus* and *erythrophthalmus* are sympatric but occupy different habitats, the song of the latter is similar to that of birds in the eastern United States, where *fuscus* is absent.

2. In California, where the two species are in closest contact, the song of *fuscus* is basically similar to that in México, but it is rarely heard except from unmated males. In California the song of *erythrophthalmus* is much simpler than in México and in the eastern United States.

3. In México the total song duration of both species is similar to that of *erythrophthalmus* from eastern United States, and about twice as long as that of *erythrophthalmus* from California.

The problem is to decide whether or not the trends in song and singing habits of the two species in California, where they are in closest contact, are closely related. As Davis

has indicated, information about the song of related genera, especially *Atlapetes* and *Melozone* is almost certain to throw light on the situation. Meanwhile, it is tempting to speculate that the close contact between the two towhees in California has resulted in interaction between them. If song duration is a critical factor in their species recognition, the shortening of the song of *erythrophthalmus* in California might be a necessary change to avoid confusion with *fuscus*, when females were selecting mates. This possibility is complicated by the rarity of song in *fuscus* in California, which seems to be associated with the maintenance of the territory and the pair bond throughout the year. The Rufous-sided Towhees on the other hand, do not maintain their territories through the winter and probably re-establish pair bonds each year (Davis, *in litt.*). Persistent singing may thus serve a real function here, and we can also see how individual variation, which is particularly marked in this species might have value in facilitating individual recognition. Whether this free use of song has in any way been responsible for the rarity of singing in *fuscus* in California we cannot at present decide, but there is clearly an intriguing problem here, which may be solved when we have more information.

SUMMARY

Variation in the songs of a single population of Brown Towhees (*Pipilo fuscus*) has been studied in Aguascalientes, México. An extended sample from one bird was also analyzed. The typical song pattern is a soft introductory *chip*, then a pause, and then a louder trill of 4–26 syllables, usually all of the same type, occasionally of two types. Song duration varies relatively little, being 1.52±0.31 seconds. Syllable duration bears an inverse relationship with the number of syllables per song, so that a song may comprise few long syllables or many short ones. Song frequency varies widely in different birds, and in the same bird at different times. Each individual uses several types of introductory and trill syllables. The latter are particularly diverse in different individuals, even if they hold adjacent territories.

The standard deviation of song characteristics in the sample from a single bird is almost as great as that of the sample from the whole population. Thus a larger sample than the one used is probably necessary to define the song characteristics of the population adequately. For more versatile singers a much greater sample will be required.

The temporal pattern of singing does not conform to expectations from Hartshorne's "continuity hypothesis." To facilitate the function of species recognition, the duration and overall temporal pattern of the song would be most suitable. For individual recognition the syllable characteristics and particularly their frequency/time structure would be most appropriate points of reference. A resemblance between syllable structure in songs of the Brown and Rufous-sided towhees is indicated and the possibility of interference between these two species in California, where they come into close contact, is discussed.

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Department of Zoology, University of California, Berkeley, California, November 11, 1959.

BREEDING BEHAVIOR IN A POPULATION OF CALIFORNIA QUAIL

By RALPH J. RAITT, JR.

The California Quail (*Lophortyx californica*) has been the subject of considerable investigation during the past 30 years, particularly from the point of view of management for hunting. Basic information on habits and general natural history was obtained by Sumner (1935). Subsequently, Glading (1938) made a nesting study of a population in the San Joaquin Valley; Emlen investigated population dynamics (1940) and movements (1939); and Emlen and Lorenz (1942) and Howard and Emlen (1942) studied social behavior, all in the Sacramento Valley.

In spite of these early studies, there has been a deficiency of basic information on density fluctuations, population turnover, productivity, movements, and social behavior in wild populations of the species. Therefore, in 1950, a study of the California Quail was initiated on an area of mixed chaparral-grassland on San Pablo Ridge, Contra Costa County, California. This investigation was conducted from 1950 to 1954 by R. E. Genelly (MS, 1955). The present study is a continuation of the same project, covering the period from 1954 through 1957. This paper presents findings of the latter four years concerning reproductive behavior in the population. Other facets of the work will be published separately.

ACKNOWLEDGMENTS

The writer wishes to express grateful acknowledgment to Dr. A. Starker Leopold of the Museum of Vertebrate Zoology, University of California, for guidance and encouragement throughout the study. Valuable advice was also given by Dr. Richard D. Taber of Montana State University and Dr. Richard E. Genelly of Humboldt State College. John Davis, A. Starker Leopold, and Lewis W. Taylor read the manuscript and offered helpful suggestions. My wife, Imogene Y. Raitt, aided in nearly all phases of the study. Weather data were furnished by Mr. Gene Smith, observer at the Grizzly Peak weather station of Berkeley, California. Victor Lewin assisted in field and laboratory work. Permission to work on restricted watershed property was granted by the East Bay Municipal Utility District. The Museum of Vertebrate Zoology of the University of California provided equipment, supplies, space, and other services, and the Department of Zoology, University of California, Berkeley, also provided supplies and equipment. To these individuals and institutions I wish to express my appreciation.

STUDY AREA

The area on which the study was conducted lies on the east slope of San Pablo Ridge, Contra Costa County. It is about one-half mile north of Inspiration Point and the same distance west of San Pablo Reservoir. Most of the study was confined to a roughly rectangular tract about ⅓ by ½ miles, including approximately 100 acres. This area is equivalent to "Area A" as defined by Genelly (1955:264). His "Area B," on the west slope of San Pablo Ridge, initially was included; but early in 1955 the United States Army began construction of an installation north of the study area, and the dirt fire road that formed the core of "Area B" was paved and subjected to very heavy traffic, thereby rendering it unsuitable as a study area. Subsequently, the study was confined to "Area A."

The area drains to the east and is made up of three ridges and two intervening canyons, with chaparral and trees on the north-facing slopes, and grass on the south-facing slopes. The topography, vegetation, climate, and land-use of the area are described in detail by Genelly (1955:263–264).

METHODS

Trapping.—The principal method of obtaining information was to capture the quail in traps, mark and release them, and then recapture them. The trapping effort resulted in 1062 captures of 444 marked birds.

Traps were made of one-inch mesh galvanized poultry netting formed into a rectangular box about two feet wide, four feet long, and two feet high. A small piece of the netting was formed into a short tunnel, semi-circular in cross section, which was inserted under one edge. The sides were fastened to the ground with spikes. Generally, traps were left in place and were set and unset by insertion and removal of the entrance tunnel. A mixture of small, whole grains, including a high percentage of millet, sold as "wild bird seed" by pet shops, was used as bait. Baiting and setting were done either in the early morning or in the late afternoon. Set traps were usually checked twice a day.

Fourteen trapping stations were utilized, but only ten were used regularly. They were all situated in locations established by Genelly, and I retained his numbering system (Genelly, 1955, fig. 1).

Marking.—A numbered leg band, obtained from the California Department of Fish and Game, was placed on each bird captured. Colored plastic numbered or lettered neck tags were attached to some of the birds for sight identification. These tags were identical to those developed and described by Genelly (*op. cit.*:265–266), who obtained valuable information by observation of birds bearing these neck tags, particularly in "Area B" where birds could be approached by car as they fed on the dirt fire road. Since the road was not used by quail after the first few months of this study and since the topography and vegetation of "Area A" permitted only infrequent observation of undisturbed quail, the application of these tags was discontinued after the second year.

Data recorded.—Age was determined by examination of the greater upper primary coverts (Sumner, 1935; Leopold, 1939). Juvenal birds were aged more precisely by noting the progress of primary feather replacement.

During the reproductive season the presence or absence of palpable eggs in the oviduct and the presence and degree of development of an incubation patch gave an indication of the stage in the breeding cycle of females.

Because of the difficulty of observing undisturbed quail on the regular study area, systematic observations of behavior were made of a covey of quail in nearby Tilden Regional Park. This covey regularly fed on lawns and in botanical gardens. Although the habitat was partly artificial, the behavioral phenomena observed in these birds in the park would probably be similar to those in the quail under more natural conditions on the nearby main study area.

PAIRING

During the greater part of the year California Quail are highly gregarious. From late August well into March the birds remain in coveys, and their behavior is strongly directed toward the maintenance of these groupings. Howard and Emlen (1942) have elucidated some of the facets of covey behavior. Throughout the spring the tendency to aggregate becomes progressively weaker until, eventually, there is complete segregation into mated pairs and lone, unmated cocks. This breakup of the coveys has been described in general terms by Sumner (1935) and by Genelly (1955). In order to supplement these observations an opportunity was taken in this study to follow the pairing of the birds in a covey numbering about 40 birds in Tilden Regional Park. Periods of time were devoted to observation on March 20, 27, and 29; April 1, 3, and 8; and May 15, 21, 22, and 24, all in 1957.

On March 20, the birds fed and bathed in the dust as a group. There was no segre-

gation into pairs, and the only indication that the breeding season was at hand was an occasional short chase of one cock by another and one apparently unsuccessful attempt at copulation. A week later on March 27 there was a slight tendency for individual males and females to feed together, but probably there was shifting about, with different birds forming the loose male-female associations at different times. Hostile behavior in the form of short chases between two males or two females were frequent and occasionally seemed to involve the protection of a paired condition against an intruder. One act of copulation was observed between members of a pair isolated from the main covey.

By March 29 pairing had advanced considerably as evidenced by the fact that the covey, when frightened, scattered mainly in pairs and re-formed in part by the congregation of pairs. Thus, although most of the time was spent grouped in a covey, some pairs had been formed within the covey. Much hostile behavior was seen, particularly among the cocks, and chases occurred almost constantly. Two full-fledged "cock fights" were observed.

The social structure and behavior on April 1 had changed little. Observations on April 3, however, revealed definite segregation of some pairs for at least part of the time. No hostile behavior was displayed against a lone male that joined a feeding pair. By April 8 the birds still showed a tendency to aggregate, but they moved to and from the main group as pairs, and most of the time a pair or two were apart from the covey. An increase in hostile behavior was evidenced by the very frequent chasing, most of which involved two males.

Nearly complete segregation into pairs had occurred by the time of the next observation on May 6. However, the various pairs still remained together in a loose group, and even formed a tight, intermixed group while dust bathing. Four instances of copulation were observed, two within two minutes. Chases of one male by another were approximately as frequent as they had been a month previously. Behavior on May 15 was much the same as on May 6 with perhaps more frequent occurrence of completely isolated pairs. On May 21 and 22, however, there was little inter-pair association or association between pairs and lone cocks. Also, the lesser number of birds visible indicated that most pairs were occupied with actual reproductive activities such as laying and incubation. Covey break-up was thus essentially complete.

In summary, the beginning of pairing occurs in late March, with a slightly more frequent association within the covey of individuals with those of the opposite sex, with increased hostile behavior, and with attempts at copulation. Throughout April and May these behavioral changes are intensified, and by late May the pairs are engaged in reproductive activities. The striking feature of this pairing process is the length of time required for its completion in the entire covey. No observations were made of any particular "pairing" display. Edminster (1954:306) states that the pair bond is formed in the covey in an unobtrusive manner. Genelly (*op. cit.*:267) observed a display in which the male "rushed" the female with feathers spread and head down. This occurred when a male approached a female confined in a "cock and hen" trap. On the other hand, he describes an instance of pairing without obvious display by two birds separated only by wire netting. The indications of the present study are that the "rush" display does not figure importantly in pair formation.

HOSTILE BEHAVIOR

"Cock fights," chases, and other hostile behavior have been mentioned. Genelly (*op. cit.*:272) has discussed the seasonal variation in the frequency of fighting and finds that spring, including March, April, May, and June, is the time during which most hostile behavior occurs. Nearly all of my observations of hostile behavior likewise were made

in the spring. Behavior associated with the establishment and maintenance of a social hierarchy in winter coveys will not be considered.

Three types of hostile behavior are recognizable among California Quail during the breeding season. These are: chasing of one bird by another; actual fights, termed "cock fights" but occurring between females also; and a form of nudging by which one bird displaces another. There are apparently no elaborate displays serving to express hostile drives as are found in many birds (Moynihan, 1955).

Chasing.—The chase is probably the most basic of the three types of hostile behavior. It is certainly the most frequently observed. This behavior consists of the aggressor lowering its head, stretching its neck out toward another bird, raising the feathers on its head and body, and running toward the other. The attacked bird seems invariably to flee from the aggressor. Seldom does any vocalization accompany a chase unless it is the aftermath of a full-fledged fight. The distance covered in a chase varies from a few steps to many yards. A very short one may consist of a simple posturing by one bird followed by a few steps in retreat on the part of the other. A long chase may consist of a rapid rush by the aggressor followed by rapid running retreat by the pursued, with frequent dodging and even short flights by one or both birds. In these longer chases the pursuer seems actually to attack the other by pecking its nape. The commonest chase is one of a few feet, in which both birds run rapidly for several steps and then return to feeding.

The length and intensity of the chase appear to depend mainly on the aggressiveness of the pursuer. The pursued bird plays a passive role, merely attempting to escape the other. One observation, however, shows that such is not invariably the case. On May 5, 1955, two pairs and a lone male were feeding on a small patch of lawn in Tilden Park. The lone cock approached one of the paired females, and her mate made a rush as if to chase away the intruder. The latter did run away but persisted in attempting to approach the female. The chase then took a circular path around the female with the mated cock attempting to keep between his mate and the other cock and the latter attempting to keep away from his pursuer and get close to the female at the same time. On this single occasion the pursuing male gave several of the "squill" calls usually associated with genuine fights. After about one minute the intruding male desisted and was driven off. Although the chasing behavior is usually simple, with a clear-cut attack and retreat, resistance on the part of the attacked bird can complicate the pattern.

Chasing may occur as the result of hostility generated in several types of social conflict. The most common context is that of a bird defending its mate against an intruder. The intruder may be an unmated male or a member of another pair. Other situations leading to chasing are the close approach by a member of the same sex during preliminary pairing, conflict between two unmated cocks later in the season, and defense of young against adults or larger young. Two males are most often involved in chases, but the chasing of one female by another is common during pairing, and occasionally a male will chase a female. Genelly (*op. cit.*:272) reports a case of a paired female chasing away a lone male.

Fighting.—Actual fights involving physical contact occur in social situations similar to those described for chasing, but they occur much less often. These fights are similar to the battles of fighting cocks. The typical "cock fight" between two California Quail has been described as follows by Genelly (*op. cit.*:271): "Opposing males face each other squarely and duel briefly but viciously with their beaks prior to leaping up and down in the cockfight. Excited and sharply-delivered 'squill calls' quite often accompany the fighting and are invariably given at the completion of the fight. Leaping apparently is an end result of sparring with the beaks to seek an advantage over the adver-

sary. . . . In the quail, the feet are not used as a weapon, the beak being the sole weapon of offense. It is most often aimed at the nape of the neck of the opponent, where it may do considerable damage if fighting continues for any length of time. The wings may also be active during a pitched battle, but these seem to serve the quail in maintaining balance rather than as a weapon." Fights begin by two birds walking erectly and rapidly toward each other. They commonly last but a few seconds, time enough for one to four leaps. The end result of a fight is the retreat of one of the contestants which is chased by his opponent for a short distance.

Although, as mentioned above, the "cock fights" occur in situations similar to those in which chases occur, the fights seem to be restricted to interactions between two birds of the same sex. No observations were made of fights between a male and a female. Most fighting occurs between two males, but occasionally fights between females were observed. In most cases the status of the cocks as to pairing was not known, but fights between two mated males and between two unmated males were seen. Whether unmated males fight with mated ones is not known, but it may be that unmated cocks are less aggressive and ordinarily flee when threatened by mated ones.

Side-by-side nudging.—The third type of hostile interaction between two quail is the side-by-side nudging. It is an inconspicuous type of behavior and was observed infrequently. This behavior appears to occur when one bird approaches too close to another bird or to its mate or young—that is, under conditions similar to those resulting in a chase. Again, males were observed to "nudge" more frequently than females.

Nudging consists of one bird approaching another one and taking a very close, side-by-side position. The two birds continue feeding, or at least pecking at the ground, but each one pecks at the ground under the head of the other. At the same time one seems to nudge or jostle the other one with its shoulder, presumably attempting to force it away. Body contact may be slight or more or less violent. Usually one bird gives ground slightly, and the two move apart and return to feeding in the normal manner. Calls were never heard accompanying this behavior. Nearly all of the observed instances of nudging were as subdued as described above, but on one occasion more aggressive behavior was involved. A male with a half-grown brood attempted to force a lone cock away from the area in which the family was feeding, and the lone male at first refused to retreat from the jostling parent. The latter then ceased pecking at the ground and began to peck at the nape of the other. The lone male ran away a few steps, and the parent returned to its family. In general, side-by-side nudging appears to occur in situations in which the birds develop less antagonism than that which results in fighting or chasing.

Conclusions.—Without further information it is impossible to draw many conclusions about the true functions and relative importance of these three types of hostile behavior. Especially needed are data of a quantitative nature and observations of marked birds the age and pairing status of which are known. It can be safely concluded, I believe, that fighting, chasing, and nudging express decreasing degrees of hostility in the order named.

COPULATORY BEHAVIOR

Copulation occurs throughout the period of pairing during the spring, probably beginning after preliminary pair bonds have been formed. In this study ten instances of copulation were observed, and the behavior was quite uniform and simple. In no case was any pre- or post-copulatory display given. Typically, the two birds foraged close together with the female leading. The female stopped feeding, settled into a low squatting position, and remained motionless. The cock, on observing the behavior of the hen, stopped feeding, straightened up, remained motionless for a very short time, and then

stepped forward and onto the back of the hen. Copulation was accomplished in a few seconds; the male stepped off and feeding was resumed immediately by both birds. In coition itself the female raised her tail into a vertical position; the male maintained his back in a nearly erect posture, bent his neck down, grasped the nape of the hen with his bill, and moved his pelvic region back and forth several times. Copulation may occur when a pair is isolated from the covey, but more often it was observed while other birds were feeding nearby. Only once was interference by other quail noticed. On May 6, 1957, a male dashed at a copulating pair, chased the other male about three yards, and remained near the female, feeding.

In the closely related Bobwhite Quail (*Colinus virginianus*) Stoddard (1931:17-18) describes a complicated "courtship" display performed by the male in front of the female preceding copulation. However, this display may function primarily in the formation of the pair bond rather than in preparation for copulation *per se*. The same may be said of Genelly's one observation of a display by a male California Quail toward a hen confined in a pen.

REPRODUCTION

The role of productivity in the dynamics of this particular population of quail will be discussed in a later paper, but special attention will be devoted here to the timing of certain phases of the reproductive process itself. A full study of reproduction would involve the collection of samples of birds of both sexes in order to examine their gonads and accessory structures. Unfortunately such collections could not be made in the present study because of adverse effects on the breeding population. Therefore, data on reproduction were obtained by examining birds trapped alive. Three main types of information may be gathered in this manner. First, it is possible to palpate shelled eggs in the uterus of the hens and to palpate soft, unshelled eggs if they are low enough in the oviduct. This method, taken from Genelly (1955:278), gives an indication as to the timing of the laying season. Another type of information is the presence or absence of an incubation patch. Possession of an incubation patch by a female is indicative of a later stage in the reproductive cycle than the presence of an egg in the oviduct. If enough hens are examined, the course of at least part of the reproductive cycle in the female population can be followed. The other phase of the reproductive cycle concerning which data were collected is the period of hatching. It is possible to estimate the ages of young quail if they are captured before they have completed the postjuvenal molt. If a sufficient number of such young birds is handled, the time of hatching of various broods can be ascertained.

Thus, by the examination of trapped birds during the breeding season, the course of laying, incubation, and hatching—on a population-wide basis—was followed. However, no information was obtained on the cycle in the males or on aspects of reproduction such as clutch size, nesting success, or hatching success.

Laying and incubation.—The reproductive status of all females examined in the breeding seasons of the four years of this study are summarized in figure 1. The solid bars represent adults, and the open ones first-year birds. A bird was considered to be laying if an egg was felt in the oviduct or uterus. Hens with no eggs but with an incubation patch were assumed to be incubating. Those without eggs were classified as "pre-laying" early in the season. It is nearly certain that each bird classified as "laying" was correctly listed, but there is likely to be error in classifying birds as "pre-laying" and incubating. Overlooking an unshelled egg in the oviduct or capturing a female soon after she had laid an egg must have occurred. Birds recorded as "pre-laying" in the third and fourth weeks of May would seem to be particularly suspect in this regard.

In spite of possible errors, the graphs do depict the course of events in the female

reproductive cycle. The graphs of Genelly (*op. cit.*:fig. 6)—from which the method of presentation used here was taken—show a very similar sequence of breeding events. Laying begins about the third week of April and continues into middle or late June. Incubation commences in the third week of May, and some birds appear still to be incubating in the first week of July. However, females incubating very late clutches were not captured, for the hatching dates of figure 2 (discussed in the next section) show that a few birds must still be incubating in late July and even into early August. Thus, the time spent by the females in various stages of reproduction lasts from mid-April through July, a period of over 100 days.

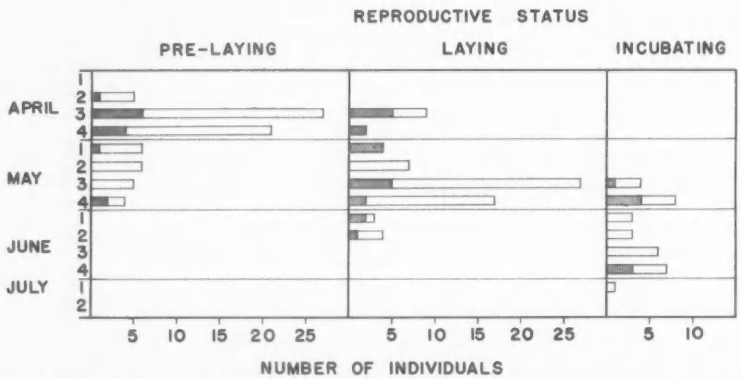

Fig. 1. Phases of the female reproductive cycle, based on data from four years. The stippled bars represent adult birds; the open bars are yearlings in their first breeding season.

If the data of figure 1 are segregated to show the pattern of each of the four years, certain annual variations may be observed. The dates on which an ovulating female was first observed were, respectively, May 5, 1954; April 14, 1955; May 1, 1956; and May 6, 1957. These dates are quite uniform except for the year 1955 when laying seemed to start much earlier than usual. Hatching dates presented in figure 2 likewise reflect the advanced date of breeding in 1955. Examination of weather records might be expected to reveal the cause of this difference, but neither precipitation nor temperatures were strikingly different in 1955. More data are necessary before the factors determining the onset of laying can be ascertained.

The dates of the cessation of laying are more uniform than are the dates of the beginning of laying. Only 14 days separate the extreme dates of the last laying hen as opposed to the 22 days separating the starting dates in 1955 and 1957. One inference to be drawn, therefore, from the dates of laying is that the earlier the population begins to lay, the longer will be its laying effort. It might further be presumed that, if laying occurs over a long period, the breeding effort would tend to be more successful. However, 1955, with a 50-day laying period, was less productive than 1954, with a 36-day period. Thus it can be concluded only that there is variation in the date of commencement of laying and that earlier seasons tend to be longer ones. What factors affect the time of laying, and what effect the length of the laying period has on productivity, are unknown.

Hatching.—The dates of hatching, shown in figure 2, were calculated from the esti-

mated ages of young birds captured alive. The method used to determine the chronological age of the juveniles is based on the uniform rate of maturation of the plumage and is described in a separate paper on plumage development. It is essentially the method of Petrides and Nestler (1943) and Genelly (1955:280). Most of the young birds were captured more than once, so that there is a check on the ageing in such cases. It will be seen in figure 2 that the first hatching dates in 1955 are earlier than those of the other years, as were the first laying dates.

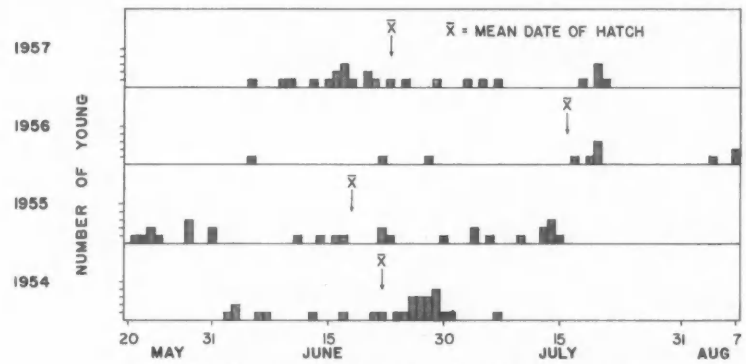

Fig. 2. Distribution of hatching dates in four consecutive years.

In 1956 three birds hatched near the end of the first week in August, two weeks later than the latest of the other three years. Genelly's data (MS) show a few late hatchings in August also. Such late hatchings are probably few in number and are the result of a belated effort to bring forth a brood by a pair that had failed once or twice earlier in the season.

SUMMARY

This paper presents observations pertaining to reproductive behavior in a population of California Quail in Contra Costa County, California. Pairing and covey break-up commenced in mid-March and were completed in May. Hostile behavior associated mostly with this period included chasing, fighting, and "side-by-side nudging." Copulation was observed several times and was uniformly simple and inconspicuous.

The periods of laying, incubation, and hatching varied from year to year in length and in time of commencement. However, in most years laying began about the third week of April and hatching ended in late July or early August, indicating a total breeding period of over three months.

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FROM FIELD AND STUDY

Temperature Fluctuation in the Smooth-billed Ani.—The occurrence of lowered body temperature in cuckoos (Cuculiformes) has not been reported, although Davis (Auk, 57, 1940:179–218) believed that the behavior of Smooth-billed Anis (*Crotophaga ani*) indicated a lack of ability to withstand low environmental temperatures. He was specifically referring to their clustering behavior during the cool morning hours and to their well known habit of perching in the sun with outstretched wings. Information on lowered body temperature with special regard to torpidity in birds has been reviewed by Bartholomew, Howell, and Cade (Condor, 59, 1957:145–155).

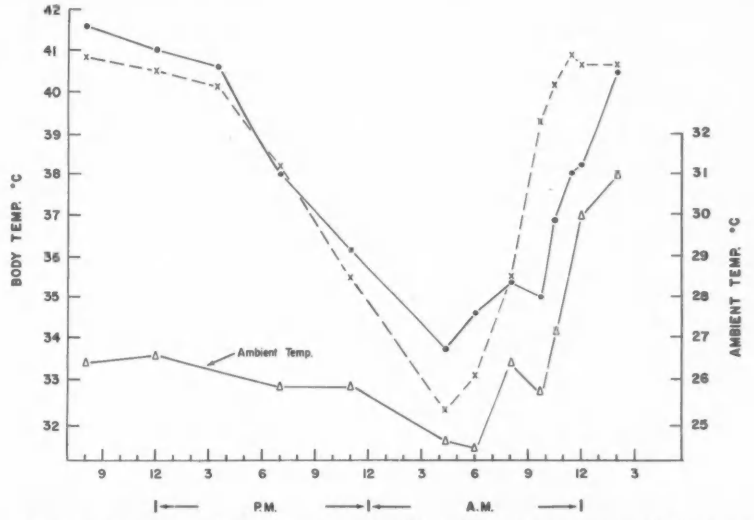

Fig. 1. Cloacal temperatures of two Smooth-billed Anis. At 7:30 a.m. one of the birds (dashed line) was placed in the sun while the other remained in a shaded situation. Ambient temperature was the same for both conditions.

Two Smooth-billed Anis were captured on the morning of August 19, 1959, near the train station at Los Frijoles, Canal Zone, Panamá. They were immediately transported to Barro Colorado Island and placed in a wire cage 6 feet long, 3 feet high, and 3 feet deep. Both birds were fairly active for the remainder of the day, but at night they became quiet and roosted with their bodies pressed close together. The following day they showed intermittent periods of activity and rest and at sundown again nestled close together on a perch.

At the time of capture the birds weighed 112.5 and 113.0 grams. This places them well above the weight range for adult females (Davis, *op. cit.*), so it was concluded that both birds were males. Both birds refused food for their entire period of captivity, which was 53 hours.

Body temperatures of these anis were read to the nearest 0.2°C. from a Schultheis thermometer inserted at least 2 centimeters into the cloaca. During the first night the birds showed no appreciable decline in body temperature. However, the second night the temperature of the birds decreased significantly from about 40.8°C. to 34.0°C. in one case and to 32.6°C. in the other (fig. 1). Even at these lowest recorded temperatures, it cannot be stated that the birds were in any way torpid. Their movements appeared to be as coordinated as those of wild birds during diurnal activity even to the extent that they were capable of flight. At 7:30 a.m. on August 21, one of the birds was placed in the sun

while the other remained in a completely shaded situation. The bird in the sun raised its body temperature about 5.6°C. in 4 hours, while the ani in the shade required 6 hours to achieve the same degree of increase. Both birds were released on the afternoon of August 21 and they immediately flew into the surrounding forest.

These cursory observations do not reveal whether or not a nocturnal temperature decline in the Smooth-billed Ani is a regular phenomenon, nor whether it is a result of starvation or of changes in environmental temperature. Possibly a condition of torpidity may be reached if the ambient temperature is sufficiently low. The feathers of this species amount to only 3.03 per cent of the body weight according to Davis (*op. cit.*) and they may prove inadequate for maintaining a large thermal difference with the environment. The temperatures of the Canal Zone may be moderate compared to those that individuals at the extremes of the range of the species might experience. If so, an ability to undergo torpor might be expected to occur in the Smooth-billed Ani.

The rate of increase of the body temperature beginning at 4:30 a.m. was extremely slow in the anis compared to that in torporous birds reported on by Bartholomew, Howell, and Cade (1957). The shaded ani required 9 hours to raise its temperature 6.4°C. The Poor-will (*Phalaenoptilus nuttallii*) studied by Bartholomew, Howell, and Cade achieved approximately the same increase in less than 3 hours with an ambient temperature of 25°C. No shivering during the temperature-increase period was observed in the anis such as is reported for the Poor-will by Howell and Bartholomew (Condor, 61, 1959:180–185). Although the sun must play some role in the heating of the birds after a nocturnal temperature decline, even the ani exposed to sunlight increased its temperature remarkably slowly. The high water vapor content of the air (relative humidity 78 per cent) reduced the amount of insolation effective for heating so that a black-bulb thermometer read only 47°C at 12 noon on August 21.

The habit in anis of several individuals pressing close together to roost no doubt reduces the heat loss and thus the rate of decline of body temperature at night. The benefits of this would be quite obvious considering the birds' poor ability rapidly to increase their temperatures.—James W. Warren, *Department of Zoology, University of California, Los Angeles, California, February 9, 1960.*

Sapsuckers Breeding in the Hualapai Mountains, Arizona.—On July 5, 1959, I collected a male Yellow-bellied Sapsucker of the race *Syphrapicus varius daggetti* (personal collection no. 23) near the 6000 foot elevation in the Hualapai Mountains, 15 miles southeast of Kingman, Mohave County, Arizona. The bird was taken from a tall oak tree near the Charles Elmer summer cabin, one mile east of the Hualapai Mountain Lodge. The owners of the cabin had requested that I get rid of the bird, because it had ruined their young Chinese Elm trees. They stated that they had seen this sapsucker every day since they had moved to their cabin one week before the date on which I took the bird. I did not measure the testes of this individual, but they were markedly enlarged.

I could not find any evidence of sapsuckers nesting in the immediate vicinity of the cabin. However, two miles south of the Elmer cabin and farther up on Aspen Peak at about the 7000 foot elevation sapsuckers were nesting. I collected a female *S. v. nuchalis* (personal collection no. 22) on the same date from a pair that was nesting twenty feet up in an aspen tree, 300 yards southeast from the main entrance of the Boy Scout camp in the Potato Patch. No attempt was made to examine the nesting cavities in the tree, but the calls of young birds were heard, and the head of a young sapsucker appeared momentarily in the entry way of one of the holes.

Both specimens were examined by Dr. Joe T. Marshall at the University of Arizona, who confirmed the identity of the two races. Dr. Thomas R. Howell of the University of California at Los Angeles also examined the specimen of the *S. v. daggetti*. Both men stated that the occurrence of this race in the Hualapai Mountains in July constituted an especially significant record.—Jon B. Coppa, *Deparment of Zoology, University of Arizona, Tucson, Arizona, January 25, 1960.*

Bird Trapped by Sedge.—On the morning of December 10, 1959, while following a dirt road through a shady ravine on Estate Bellevue, St. Croix, Virgin Islands, I saw a bird in distress beside the track. It was flapping about in some low vegetation, and I thought at first it was sick or had been injured. On reaching it I found a Pearly-eyed Thrasher, *Margarops fuscatus* (locally called "T'rush"),

with its tail feathers firmly tangled in the slightly rough leaves and stems of a slender sedge, later determined to be *Scleria lithosperma*, by Dr. A. J. Oakes, Jr. Apparently the bird had been feeding on the ground, and its rather lax rectrices had been caught by the sedge, much as children catch a companion's hair by twisting a grass panicle, stripped of seeds, against it.

The bird was able to bite and had a good grip with its feet, but it could neither walk nor fly. It was an adult male (skull completely ossified) with a practically empty gut, but it is believed to have been suffering more from lack of water than food. Judging from the appearance of the bird and of the scratched-up sedge area, the bird must have been trapped not later than the previous day.—R. M. Bond, *Kingshill, St. Croix, Virgin Islands, January 11, 1960.*

New Records of Raptors from Jalisco, México.—While on a trip by jeep from La Huerta northward along the Jaliscan coast to El Tuito, in February, 1959, the authors had the good fortune to collect specimens of the Hook-billed Kite (*Chondrohierax uncinatus*), the Roadside Hawk (*Buteo magnirostris*), and the Collared Forest-Falcon (*Micrastur semitorquatus*), near Tomatlán. These specimens seem to represent new additions to the known avifauna of the State of Jalisco, as shown in the Mexican Check-list (Pt. I, Pac. Coast Avif. No. 29, 1950).

The Roadside Hawks, a pair, agree in all essential characters with topotypes of *Buteo magnirostris xantusi* van Rossem, from the Río Armería, Colima, and represent a slight northward extension of the known range of the species. *Chondrohierax uncinatus uncinatus* was recorded previously only from the states of Sinaloa, Guerrero, and México, although the senior author has an unrecorded female from El Tuito, Jalisco. *Micrastur semitorquatus* was known previously from Sinaloa south to Chiapas on the Pacific coast of México, but with no known specimens from Jalisco. This specimen nicely fills the apparent gap.

It was especially interesting to us to collect both the "highland" Northern Pygmy Owl (*Glaucidium gnoma*) and the "Humid Tropical" or "Arid Lower Tropical" Least Pygmy Owl (*G. minutissimum*) on opposite sides of the same small, but steep, barranca in the lower Sierra de Autlán, in the course of the same explorations. The vegetation was similar on both sides, although the oaks were denser where *gnoma* was shot; however, *minutissimum* was actually closer to the small stand of young pines on a ridge! The latter was also taken in a grove of pines in central Colima.

In the same general region, the junior author took a Barred Owl (*Strix varia*) in the upper part of the Sierra de Autlán, and the Sharp-shinned Hawk (*Accipiter striatus suttoni*), the Spotted Owl (*Strix occidentalis*), and the Stygian Owl (*Asio stygius*) on the Volcán de Nieve (the Cerro Nevado de Colima—the "Sierra Nevada de Colima" *auctorum*). The two last-mentioned have not been taken previously in Jalisco, and the record of the Spotted Owl represents a considerable westward extension of range from Cerro Tancítaro, Michoacán.—Allan R. Phillips and William J. Schaldach, Jr., *Western Foundation of Vertebrate Zoology, Los Angeles, California, January 19, 1960.*

Eating of Sand by Blue Jays.—Family groups of Blue Jays (*Cyanocitta cristata*) have come to a sand pile in our yard in Bethesda, Maryland, during the fall and winter months of several years, but it was not until a period of successive snowstorms in February and March, 1960, that I was able to observe in detail their habit of eating sand. Five jays, for example, arrived soon after sunrise on February 14. The sand was covered by 4 inches of fresh snow and the jays hopped about as if searching until one of them scooped out a hole by a rock. The others came over immediately to peck down inside. On March 3, two jays arrived at 7 a.m. in the midst of a snowstorm and alighted above the sand pile in 8 inches of fresh snow. They floundered helplessly, then flew away. As one of the jays perched on a limb, the other one came and fed it in what I interpreted to be courtship feeding. Two of the jays did appear to be closely associated on successive mornings. Thus a pair of jays came at 7:15 a.m. on March 4, worked together as they scooped away the snow from the base of a child's toy, then pecked down at the sand. The pair left after 6 minutes. At 7:30 a.m., however, four jays arrived over the sand pile and two of them flew away immediately, leaving the other two to work, after a few conflicts among them, at separate holes. I wondered if the paired birds had not brought their offspring of a previous year to the sand pile. Events on March 6 gave further suggestion that the jays were a family group. The pair came to the pile at 6:55 a.m., fed peacefully, and flew away; but at 7:05 a.m.

five jays were back at the same place. Two of them (the pair?) left at once while the other three pecked down into holes over the sand pile, frequently rising several feet into the air as they quarreled with each other.

There was no evidence that the Blue Jays were finding food on these occasions. They were not picking up objects of appreciable size, and other species of birds, including Starlings (*Sturnus vulgaris*), which came in numbers to our adjacent feeding station, showed no interest in the sand pile. In order to obtain more precise observations, I placed some washed sand on a bare log above the snow-covered pile on March 7. The pair of jays came down immediately. One of them picked up 100 or more grains or small aggregates of sand and two other jays, which succeeded each other on the log shortly afterward, took 15 to 20 billfulls from the center of the head of sand, tipping their heads sideways to do so. One of these latter jays fed on snow at the same time. During a snowstorm on March 10, the pair came at 6:45 a.m. and fed peacefully on the log where I had put additional sand. The other three jays which arrived 5 minutes later made an amusing sight, for, as one drove another from the log, the evicted jay would land belly-deep in fresh snow, then struggle with outspread wings to free itself. Altogether, there were jays at the heap of pure sand from 6:40 until 6:55 a.m. The punctuality of their arrivals was indicated by their coming for sand on the following two days at 6:40 and 6:35 a.m., respectively.

Beal, in a study of the food of the Blue Jay (quoted by Bent, U. S. Nat. Mus. Bull., No. 191, 1946:480 pp.) stated that "One of the first points to attract attention in examining these stomachs was the large quantity of mineral matter, averaging 14 per cent of the total contents." The nature of the mineral matter taken by the jays in our yard was not always obvious. On mornings after the foregoing observations were made, for example, there were patches of the sand pile which were bare of snow and the jays visited these in seeming preference to the pure sand on the log. I wondered whether they really preferred a mixture of sand and dirt. A fresh snowfall on March 17 provided an opportunity for an additional experiment in which I placed a mixture of sand and dirt at one end of the log and of pure sand at the other. Five jays alighted on the log between 6:35 and 6:55 a.m. All fed on the heap of sand and none of them on the mixture, even though some of them perched in the middle of it. My observations and experiments were far from complete. It would appear, however, that Blue Jays eat sand on a daily basis in the fall and winter and my interpretation is that the habit is related to the digestion of grains, acorns, or other hard fare.—LAWRENCE KILHAM, *Bethesda, Maryland, April 12, 1960.*

A Drongo New to the Philippine List.—In January of 1959, through the kind cooperation of Dr. Dwain W. Warner and Mr. Robert W. Dickerman of the University of Minnesota Museum of Natural History, 475 specimens from the historic Menage collection of Philippine birds were exchanged to Carnegie Museum. Among these specimens are three drongos from the island of Sulu, labelled "*Chibia borneensis*" (= *Dicrurus hottentottus suluensis*). Two of these are labelled as adults, and one as "juv." Although the latter specimen differs conspicuously from the two adults, these differences were apparently attributed to immaturity by the collectors and subsequent workers who have handled these drongos. Believing that the identification of this specimen, Menage collection no. 1581, was incorrect, I checked it against the series of drongos in the American Museum of Natural History. It proves to be a typical example of the Crow-billed Drongo, *Dicrurus annectans*, the first record of this species from the Philippines. I am indebted to Dr. Charles Vaurie for confirming my identification.

The Crow-billed Drongo is the most highly migratory member of its family (Vaurie, Bull. Amer. Mus. Nat. Hist., 93, 1949:267). It breeds from the foothills of the Himalayas in Nepal and Assam southeast to northern Thailand, migrating through the Malay Peninsula and adjacent islands to Sumatra, Java, and Borneo. The easternmost previously known record appears to be the specimen from Sandakan, North Borneo, listed by Vaurie (*loc. cit.*), a record not mentioned in Smythies' Borneo check-list (Sarawak Mus. Jour., 7, 1957:774).

The Menage specimen was collected on the island of Sulu, 200 miles east of Sandakan, by F. S. Bourns and D. C. Worcester, on September 30, 1891. It is sexed as female and exhibits the white tips to abdominal feathers, under tail coverts, and under wing coverts typical of young birds of this species. The Sandakan specimen is also an immature female. The iris of the Sulu bird was described as "dark

cherry red," and the legs, feet, nails and bill as black. The stomach contained grasshoppers. The specimen is a taken-down mount in excellent condition.

In Delacour and Mayr's key to Philippine drongos (Birds of the Philippines, 1946:250), *Dicrurus annectans* would key out to *D. b. balicassius*. The latter species does not occur in the Sulu Archipelago, but it is possible that other specimens of *annectans* from elsewhere in the Philippines may repose unrecognized in collections. The two species may be separated by the shape of the tail, which is scarcely forked in *balicassius* and definitely forked, with terminal half of outer rectrices outcurving, in *annectans*. In addition, *annectans* has a proportionately smaller bill and is less brilliantly iridescent than *balicassius*.

In discussing the drongos in the Menage collection it may be appropriate to mention the fact that two "cotypes" (more properly syntypes) of *Chibia menagei* Bourns and Worcester (= *Dicrurus hottentottus menagei*) from Badajoz, Tablas Island, are now in Carnegie Museum. Vaurie (*op. cit.*: 313) listed as "cotypes" two specimens in the United States National Museum. Bourns and Worcester were in the habit of attaching red type labels to a series of specimens rather than to a single holotype. —KENNETH C. PARKES, *Carnegie Museum, Pittsburgh, Pennsylvania, January 28, 1960.*

Acorn Woodpecker Resident East of the Sierra Nevada in California.—The Acorn Woodpecker (*Balanosphyra formicivora*) has been considered a resident in California only in that part of the state lying west of the Sierra Nevada where oak trees are present. There is only one record of occurrence on the east side of the Sierra in California; a single specimen was taken near Lone Pine, Inyo County, on September 8 (Grinnell and Miller, Pac. Coast Avif. No. 27, 1944:232). In their work on the vertebrates of the Lassen Peak area, Grinnell, Dixon, and Linsdale (Univ. Calif. Publ. Zool., 35:250) found no Acorn Woodpeckers east of the western edge of the yellow pine belt.

On June 4, 1959, we observed an Acorn Woodpecker near a stand of black oaks (*Quercus kelloggii*) about 5 miles southeast of Janesville, Lassen County, California, along highway 395. On June 21, another individual was found in the same locality, and four others were observed in the town of Janesville. Further observations on June 28 revealed the presence of a nest containing young in a black oak one-half mile southwest of Janesville. In this area we found three dead ponderosa pines (*Pinus ponderosa*) covered with typical nut-storage holes, many of which were filled with acorns. The ground beneath one of the trees was covered with acorn shells to a depth of over two inches. Black oaks were abundant in this area.

Specimens were collected at Janesville for subspecific identification. A male and female were taken on July 4, 1959, and four females were collected on October 2. Comparison of these specimens with others at the Museum of Vertebrate Zoology show that they belong to *Balanosphyra formicivora bairdi*. All were typical of this subspecies except the two specimens collected in July; these had orange-red napes instead of the bright red of all other specimens examined.

Black oaks occur in a continuous stand along the base of the Sierra from seven miles south of Janesville north to Susanville. From Susanville the stand extends west for a short distance along the lower portion of the Susan River and east along Antelope Mountain to Willow Creek. No other oaks occur within several miles of this stand. The Acorn Woodpecker population in the Janesville-Susanville area apparently is therefore an isolated one.—STURGIS MCKEEVER, *Department of Zoology, University of California, Davis,* and LOWELL ADAMS, *Southwest Forest and Range Experiment Station, United States Forest Service, Berkeley, California, December 4, 1959.*

Brown Thrasher in Death Valley, California.—A Brown Thrasher (*Toxostoma rufum*) was found dead near Furnace Creek Ranch, in the center of Death Valley, Inyo County, California, on November 1, 1959. The bird had been dead for several days, but the skin was preserved and sent to the Museum of Vertebrate Zoology at Berkeley, California, for identification; racial identification proved to be impossible. This species has now been reported several times in California as a rare winter visitor and most recently at San Diego by Morley, on November 26 and 27 (Condor, 61, 1959:374). —ROLAND H. WAUER, *Death Valley National Monument, California, November 15, 1959.*

Nesting of the Golden Eagle in the Central Brooks Range of Arctic Alaska.—There are apparently no detailed records of the nesting of the Golden Eagle (*Aquila chrysaëtos*) in the central Brooks Range of arctic Alaska. Irving (Arctic, 6, 1953:41), in noting the status of birds in the Anaktuvuk Pass region, indicates that the Golden Eagle breeds there but offers no further information relative to the nesting behavior of that species in the area. In fact, the only documented reference to its breeding anywhere in the Brooks Range appears to be that of Bailey (Colorado Mus. Nat. Hist., Popular Series, No. 8, 1948:182) who states that "Two eggs in the Hanna collection were secured from a nest on a steep bluff in the mountains south of Barter Island on May 6, 1947."

Late in the summer of 1959, Gene Wallace and John Severe reported to me that some weeks earlier they had discovered the nest of a "large eagle or hawk" while oil prospecting along the treeless, northern margin of the Brooks Range near Anaktuvuk Pass. On August 10, 1959, I accompanied them in a helicopter to the nest site, 5 air miles due west of the Anaktuvuk River, at about 68° 18′ N, 151° 43′ W. That location is nearly 40 air miles from the nearest spruce timber to the south. As we approached, an adult Golden Eagle was seen flying from a cavity in a cliff, and closer observations, at distances of less than 100 feet, revealed a crevice occupied by a single juvenal eagle, apparently almost fully fledged.

In that locality the northern front of the Brooks Range consists of a high wall which breaks sharply to the rolling foothills of the arctic slope. The nest was situated 3900 feet above sea level near the top of the north-facing rampart and about 240 feet above the base of a nearly vertical limestone cliff. Below the nesting cliff a precipitous talus slope extended downward to the floor of a small valley 1000 feet below. The narrow nest crevice appeared to be about 4 or 5 feet in horizontal depth and of nearly the same dimensions in height. Few sticks or other debris of any kind were present within the crevice. The following day we returned to the nest site and observed two adult Golden Eagles coursing together along the face of the cliff. One carried a small mammal in its talons, apparently a ground squirrel (*Citellus parryi*).

Conclusions regarding arctic variations in the usual nesting behavior of the Golden Eagle are admittedly hazardous when based on a single record. It is noteworthy, however, that this nest differed considerably from the usual bulky structure of sticks ordinarily associated with the species. Although well north of tree line, numerous willows growing along small streams in the vicinity of the nest would presumably provide abundant raw materials for nest building. The relative maturity of the fledgling eagle led me to think that it had left the original nest location to take up temporary residence in the previously described crevice. Wallace and Severe stated, however, that they had discovered the young bird in the same rock cavity several weeks before. The egg or eggs had apparently been deposited in a scanty nest on the rocky floor of the crevice. Also, although we did not examine the surrounding cliffs in great detail, we observed no alternate nests, the construction of which is characteristic of Golden Eagles when cliffs are used for nest sites. However, if other nests of the type observed were present, they would be difficult to find.

The apparent age of the immature eagle on the tenth of August indicates that hatching probably occurred about the first of June. This estimate agrees with Bailey's reference to the finding of eggs of this species on May 6 in the mountains south of Barter Island. These two records tempt one to postulate that, in the Brooks Range, the Golden Eagle normally nests at the end of April or very early in May.—John M. Campbell, *The George Washington University, Washington, D.C., January 15, 1960.*

Correction.—Recently I reported (Condor, 62, 1960:70) remains of the California Condor (*Gymnogyps californianus*) from the late Pleistocene of Rampart Cave in Arizona and expressed the opinion that this was the first authentic record of condors from that state (sight records are not considered "authentic"). I was in error. Lyndon Hargrave kindly calls my attention to a publication overlooked by me (Plateau, 29, 1956:44–45) in which Raymond de Saussure reports condor remains from Recent cave deposits of northern Arizona. The Rampart Cave bones are, however, the only fossil records for the area. My apologies to Mr. de Saussure and thanks to Mr. Hargrave.—Loye Miller, *University of California, Los Angeles, California, March 15, 1960.*

NOTES AND NEWS

A conference on the potential role of birds in the epidemiology of certain viruses affecting man was held at the National Institute of Health on April 4, 1960. The purpose was to bring ornithologists and virologists together in a joint effort to suggest solutions for these problems. A result of the discussions was recognition that many ornithological aspects need more research. For example, dates of arrival and of departure, numbers of migrants, distribution in South America and in southern United States, and also several physiological aspects are important problems that ornithologists might explore in more detail. The Public Health Service supports basic research that often has intrinsic ornithological value. Information about applications for grants may be obtained from: Research Grants Division, U.S. Public Health Service, Bethesda 14, Maryland. The ornithologists present at the conference were Dr. David E. Davis, Pennsylvania State University, University Park, Pennsylvania; Mr. Allan Duvall, Patuxent Research Refuge, Laurel, Maryland; Mr. William H. Gunn, Ontario Society of Naturalists, Toronto, Canada; and Dr. Herbert Friedmann, U.S. National Museum, Washington 25, D.C.

The Nature Conservancy has been active for some years in acquiring and setting aside nature preserves in America for the conservation of unspoiled natural habitats. Such an area is the Northern California Coast Range Preserve in the Eel River drainage which has an exceptionally large remaining stand of pure Douglas fir forest. A part of the large preserve is dedicated to Joseph Grinnell and is set aside exclusively for research studies in natural history. Many friends and colleagues of Grinnell have contributed to this undertaking, and 71 acres, at $33 an acre, have already been provided for this purpose. Cooper Society members as former associates of Grinnell will be interested in the success of this venture in conservation and may wish opportunity to take part.—A.H.M.

Papers on the scientific program of the thirty-first annual meeting of the Cooper Ornithological Society in Los Angeles on May 6 and 7, 1960, were: "Forecasting the Quail Crop," by Ian I. McMillan; "Habits of Scaled and Gambel Quail in New Mexico," by Ralph J. Raitt; "Specimen Identification of Flycatchers in the *Empidonax hammondii–wrightii–griseus* Complex," by Ned K. Johnson; "Reproduction and Ecology of the Bronze-winged Jacana (*Metopidius indicus*)," by Gerald Collier; "A Day with the Penguins and Shearwaters on Phillip Island, Australia," by Junea W. Kelly; "Interrelation of Rainfall and Innate Breeding Cycles in Andean Sparrows," by Alden H. Miller; "Comparison of Premigratory Testicular Growth and Changes in Body Weight in Three Taxa of *Leucosticte*," by James R. King; "An Investigation of the Termination of the Gonadal and Metabolic Refractory Periods in the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*)," by James McCammon; "Feather Microcharacters, a Key to Species Identification," by Lyndon L. Hargrave; "The Taxonomic Significance of the Hyoid Bones and Tongue Muscles of Passerine Birds," by William George; "Territorial Relationships between Cardinals and Pyrrhuloxias," by Patrick J. Gould; "A Review of North American Hybrid Hummingbirds," by Richard C. Banks and Ned K. Johnson; "Distributional Patterns of the Birds of Sierra Ancha, Gila County, Arizona," by R. Roy Johnson; "Life History of the Glaucous-winged Gull," by Ernest S. Booth; "The Value of Aviculture in Ornithology and Bird Preservation," by Phyllis Barclay-Smith; "The Usual and the Odd among Birds of the Barrow Region, Northern Alaska," by Frank A. Pitelka; "Observations on the White-rumped Sandpiper at Point Barrow, Alaska," by Richard T. Holmes and Frank A. Pitelka; "Transequatorial Migration," by A. J. Marshall; "East African Birds," by F. Edmond-Blanc; "Nest-building in the Village Weaverbird of Africa," by Nicholas E. and Elsie C. Collias; "Species Limits in Woodpeckers of the Genus *Centurus* in Northern Mexico," by Robert K. Selander; "Experiments on Nesting Behavior of the Laysan and Black-footed Albatrosses," by Thomas R. Howell and George A. Bartholomew; "Aspects of the Breeding Biology of the Rhinoceras Auklet," by Frank Richardson; "Life History of the White-winged Junco," by N. R. Whitney; "Three-year Histories of Banded Pairs of Brown Towhees," by Joe T. Marshall, Jr.; "Seasonal Changes in Morphology of the Rufous-sided Towhee," by John Davis; "Growth and Weight Curves in the Young of the White-winged Dove," by Ernest R. Tinkham; "Trichomoniasis in Doves," by Henry M. Weber; "The Bionomics of the White-winged Dove in the Arizona Sahuaro Desert, 1940–1960," by Ernest R. Tinkham.

COOPER ORNITHOLOGICAL SOCIETY, INC.
STATEMENT OF CASH RECEIPTS AND DISBURSEMENTS
FOR THE YEAR ENDED DECEMBER 31, 1959

CASH IN BANK, DECEMBER 31, 1958			$ 8,638.04
ADD: CASH RECEIPTS			
General Publication Fund			
Membership dues, regular and sustaining	$5,259.95		
Subscriptions for The Condor	1,140.21		
Condor sales	132.40		
Phonograph record sales (3 records sold)	22.50		
Dividends and interest received on endowment funds invested (Note A)	5,240.66		
Dividends received from Harry R. Painton legacy (Note B)	6,715.57		
Contributions received for the publication of The Condor	100.00		
Other cash receipts	294.46	$18,905.75	
Avifauna Fund			
Avifauna sales, net (Note C)	$1,045.63		
Transfer from General Publication Fund	4,000.00		
Contributions received	1,300.00		
Other cash receipts	531.31	6,876.94	
Endowment Fund			
Life memberships and installment payments received on life memberships	$1,051.00		
Contributions received	100.00		
Other cash receipts	1,607.41	2,758.41	28,541.10
			37,179.14
DEDUCT: CASH DISBURSEMENTS			
General Publication Fund			
Publication Costs of The Condor			
Printing	$9,903.58		
Engraving	1,855.88	$11,759.46	
Cost of phonograph records		3.46	
Administrative Expenses			
Northern division	$ 69.20		
Southern division	128.09		
Annual meeting	440.04		
Business manager	223.02		
Accounting	150.00		
Treasurer	394.91		
Editor	757.71		
Other disbursements	1,078.70	3,241.67	
Tansfer to Avifauna Fund		4,000.00	
Avifauna Fund			
Sales tax paid	$ 29.57		
Printing and engraving	5,794.24		
Shipping and postage	79.69		
Other disbursements	317.70	6,221.20	
Endowment Fund			
Purchase of corporate securities	$3,802.10	3,802.10	29,027.89
CASH IN BANK, DECEMBER 31, 1959			$ 8,151.25

CASH IN BANK ALLOCATED TO FUNDS AS FOLLOWS:	Dec. 31, 1958	Dec. 31, 1959
General Publication Fund	$1,619.27	$ 1,520.43
Avifauna Fund	5,138.44	5,794.18
Endowment Fund	1,880.33	836.64
TOTAL	$8,638.04	$ 8,151.25

Note A: At December 31, 1959, the business manager had in his custody endowment funds invested in corporate securities which cost $58,819.84, and had a market value of $178,623.00. This endowment fund includes contributions received in the names of Florence M. Bailey, Louis B. Bishop, Albert E. Colburn, Joseph Grinnell, A. Brazier Howell, and Harry R. Painton.

Note B: Dividends received from the Harry R. Painton legacy represent the amount accumulated during the four years of litigation in connection with the settlement of the Harry R. Painton estate.

Note C: At December 31, 1959, the Society had a stock of Avifaunas for which the total of quoted list prices was $35,823.00.

C. V. DUFF, *Business Manager*

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OF THE

COOPER ORNITHOLOGICAL SOCIETY

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Revised to June 15, 1960

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A

Abbott, Jackson M., 1100 Doter Dr., Waynewood, Alexandria, Va. 1957.

Abowitz, Murray, 6333 Wilshire Blvd., Suite 301, Los Angeles 48, Calif. 1958.

Adams, Capt. Claude T., W.A.D.C., Area B, Box 8607, Wright-Patterson AFB, Ohio. 1951.

Adams, Heman P., 218 Main St., Glenville, W. Va. 1956 (1960) [S.].

Adams, Lowell, Pac. Southwest Forest & Range Exp. Sta., Box 245, Berkeley 1, Calif. 1960.

Adams, William H., Jr., Route 2, Madisonville, Tenn. 1952 (1958) [L.].

Adamson, Francis H. H., Banco de Londres y America del Sud, Reconquista No. 157, Buenos Aires, Argentina. 1959 (1959) [S.].

Adamson, Harry C., 995 Carol Lane, Lafayette, Calif. 1960.

Adelson, Richard H., Remsen Lane, R.F.D. 1, Oyster Bay, Muttontown, L. I., N. Y. 1950 (1958) [S.].

Ahmanson, Howard, 3701 Wilshire Blvd., Los Angeles 5, Calif. 1959 (1960) [S.].

Aiken, Carl H., III, 3767 Georgetown, Houston 5, Texas. 1959.

Albro, Mary S., 29 Mosswood Rd., Berkeley 4, Calif. 1928.

Alcorn, Gordon D., College of Puget Sound, Tacoma 6, Wash. 1942.

Alcorn, Joseph R., 45 W. Fairview St., Fallon, Nev. 1939 (1947) [L.].

Alderson, George, 6230 S.E. 36th Ave., Portland 2, Ore. 1959.

Aldrich, Elmer C., 5631 Camellia Ave., Sacramento 19, Calif. 1935.

Aldrich, John W., 7725 Lakeview Dr., Falls Church, Va. 1942 (1950) [S.].

Alexander, Gordon, Biology Dept., Univ. Colorado, Boulder, Colo. 1941 (1956) [S.].

Alexander, Helen M., 2121 W. 9th St., Los Angeles 6, Calif. 1958.

Alexander, Wilfrid B., Dept. Zoological Field Studies, Edward Grey Inst., Botanic Gardens, Oxford, England. 1959.

Ali, Salim A., 33 Pali Hill, Bombay Suburban Dist., Bandra, India. 1959.
Allen, Alice G., 143 W. Acacia, Apt. 4, Stockton 3, Calif. 1957.
Allen, Arthur A., Laboratory of Ornithology, Fernow Hall, Cornell Univ., Ithaca, N.Y. 1911.
Allen, Esther C., Camarillo State Hospital, Camarillo, Calif. 1951.
Allen, George A., 1328 Allen Park Dr., Salt Lake City 5, Utah. 1957.
Allen, Herbert E., 822 Wild Rose Ave., Monrovia, Calif. 1956.
Allin, Albert E., 404 S. Norah St., Fort William, Ontario, Canada. 1956.
Alperin, Irwin M., 187 Cedar Lane, Babylon, L. I., N.Y. 1947.
Altmann, Stuart A., Biological Labs., Harvard Univ., Cambridge 38, Mass. 1955.
Alvarez del Toro, Miguel, Apartado Postal No. 6, Tuxtla Gutierrez, Chiapas, Mexico. 1948.
Amadon, Dean, American Museum of Natural History, Central Park West at 79th St., New York 24, N.Y. 1943.
Anderson, Allen E., Wildlife Research Unit, Colorado State Univ., Fort Collins, Colo. 1956.
Anderson, Anders H., 3221 E. Kleindale Rd., Tucson, Ariz. 1932 (1949) [S.].
Anderson, Byron C., 123 D St., Salt Lake City 3, Utah. 1960.
Anderson, Earl A., 7335 N. Odell Ave., Chicago 31, Ill. 1952 (1958) [S.].
Anderson, Eugene N., Jr., 318 23rd St., Santa Monica, Calif. 1957.
Anderson, Frank G., Sociology Dept., Univ. Maryland, College Park, Md. 1951.
Anderson, Sydney, Mus. Nat. Hist., Univ. Kansas, Lawrence, Kans. 1957.
Anderson, William, Markay Motel, Gridley, Calif. 1948 (1951) [S.].
Andrews, Arthur A., 75 Penfield Crescent, Brighton Sta., Rochester 10, N.Y. 1927 (1949) [S.].
Annan, Ormsby, 270 Birch St., Winnetka, Ill. 1951 (1954) [L.].
Antevs, Ada, "The Corral," Globe, Ariz. 1946 (1947) [L.].
Appelman, F. J., Stichting Rotterdamsche Diergaarde, Rotterdam, Netherlands. 1953.
Applegarth, John H., Box 10, California Polytechnic College, San Luis Obispo, Calif. 1937.
Arbib, Robert S., Jr., 128 Lawn Terrace, Mamaroneck, N.Y. 1947.
Argante, Mrs. A. J., 1728 Richmond St., Apt. 13, Sacramento 25, Calif. 1955.
Armington, Sven, Sveriges Ornitologiska Förening, Ostermalmsgatan 65, Stockholm, Ö, Sweden. 1951.
Armstrong, Rev. E. A., St. Mark's Vicarage, Barton Rd., Cambridge, England. 1959.
Armstrong, Fairbearn H., Naches Ranger Sta., Naches, Wash. 1954.
Armstrong, Virginia, Old Concord Rd., South Lincoln, Mass. 1947 (1960) [S.].
Arnold, Hubert A., 533 E St., Davis, Calif. 1956.
Arnold, John R., 834 W. Mariposa St., Stockton 4, Calif. 1930 (1960) [S.].
Arnold, Ralph, 324 W. Arrelloga, Santa Barbara, Calif. 1893.
Arny, Samuel A., 7432 Hamlet St., Springfield, Va. 1947.
Aronoff, Arthur E., Zoology Dept., Univ. Michigan, Ann Arbor, Mich. 1948 (1955) [L.].
Arsenault, Barbara J., 16025 Miami Way, Pacific Palisades, Calif. 1954.
Arvey, M. Dale, Biology Dept., Long Beach State College, 6101 E. 7th St., Long Beach 4, Calif. 1953 (1960) [S.].
Ashcraft, Granville P., Box 438, Etna, Calif. 1940.
Atsatt, Sarah R., 1130 N. Monterey St., Alhambra, Calif. 1911 (1957) [S.].
Austin, Enid K., 1116 Mandana Blvd., Oakland 10, Calif. 1939.
Austin, Oliver L., Jr., Florida State Museum, Gainesville, Fla. 1958.
Austing, Ron, R.R. 1, Strimple Rd., Harrison, Ohio. 1960.
Avent, Carrie P., Minter City, Miss. 1957.

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Badger, Lester R., Rt. 1, Box 528, Excelsior, Minn. 1958.
Badger, M. C., Rt. 1, Box 98, Santa Paula, Calif. 1915.
Baepler, Donald H., Science & Math. Div., Central Washington College of Education, Ellensburg, Wash. 1956.
Bailey, Alfred M., Colorado Mus. Nat. Hist., Denver 6, Colo. 1917.
Bailey, Laura B., Rockbridge, Alum Springs, Rt. 2, Goshen, Va. 1915 (1920) [L.].
Bailey, Richard, 1107 High Court, Berkeley 8, Calif. 1949.
Baird, James, Norman Bird Sanctuary, Third Beach Rd., Newport, R. I. 1957 (1957) [L.].
Baker, John H., 169 E. 78th St., New York 21, N.Y. 1930 (1959) [S.].
Baker, Paul S., 21 Woodlot Lane, Huntington, L. I., N.Y. 1945 (1960) [S.].
Baker, Rollin H., The Museum, Michigan State Univ., East Lansing, Mich. 1946.
Baker, William C., 559 Euclid St., Salem, Ohio. 1959.
Bakker, Gerhard, Jr., 450 W. Ave. 43, Los Angeles 65, Calif. 1954.
Baldwin, Paul H., 1205 Remington St., Fort Collins, Colo. 1943.
Baldwin, William G., Eye & Ear Hospital, Box 1627, Wenatchee, Wash. 1953.
Balsom, Mrs. Amos P., 2209 E. Stratford Court, Milwaukee 11, Wis. 1948.
Baltzar, Evelyn C., 15057 Starbruck Ave., Whittier, Calif. 1946.

Banks, Richard C., Museum of Vertebrate Zoology, Berkeley 4, Calif. 1956.
Bannerman, David A., Boreland of Southwick, by Dumfries, Scotland. 1959.
Bard, Fred G., Saskatchewan Mus. Nat. Hist., Regina, Saskatchewan, Canada. 1948.
Barlow, Jon C., Zoology Dept., Univ. Kansas, Lawrence, Kans. 1959.
Barnes, F. R., 4282 Maple Ave., Oakland 2, Calif. 1947.
Barrett, Vernon, 1300 Chelton Way, South Pasadena, Calif. 1948 (1958) [L.]
Bartel, James N., 206 N. St. Andrews Pl., Apt. 6, Los Angeles 4, Calif. 1951.
Bartel, Janice R., 206 N. St. Andrews Pl., Apt. 6, Los Angeles 4, Calif. 1960.
Barth, R. H., Jr., Biological Labs., Harvard Univ., Cambridge 38, Mass. 1957.
Bartholomew, George A., Jr., Zoology Dept., Univ. California, Los Angeles 24, Calif. 1942.
Bartleson, Fred D., Jr., 6455 J Pine Valley, U.S.A.F. Academy, Colo. 1953.
Bartlett, Lawrence M., Zoology Dept., Univ. Massachusetts, Amherst, Mass. 1957.
Basey, Harold E., Box 419, Orosi, Calif. 1954.
Bassett, Frank N., 722 N. Orange Dr., Los Angeles 38, Calif. 1919.
Battles, Carroll D., 2347 S. Highland Ave., Los Angeles 16, Calif. 1924 (1957) [S.].
Batts, H. Lewis, Jr., Kalamazoo College, Kalamazoo, Mich. 1947 (1959) [L.].
Bauman, Donald F., 1307 N. Spadra Rd., Fullerton, Calif. 1957.
Baumgardt, John H., 7838 N. Glencoe Heights Dr., Glendora, Calif. 1937.
Baumgarten, Gail G., 11990 Laurelwood Dr., Studio City, Calif. 1950.
Baxter, Evelyn V., The Grove, Upper Largo, Fifeshire, Scotland. 1959.
Baylor, Leslie M., 1302 S. 4th Ave., Pocatello, Idaho. 1958.
Beals, Edward, Botany Dept., Univ. Wisconsin, Madison 6, Wis. 1957.
Bean, Emory L., Calif. State Polytechnic College, Box 608, San Luis Obispo, Calif. 1959 (1959) [S.].
Beaudette, Palmer T., R.F.D. 1, Box 480, Solvang, Calif. 1956 (1956) [S.].
Beckwith, William C., 1107 Chautauqua Blvd., Pacific Palisades, Calif. 1958.
Beebe, Frank L., R.R. 1, 3214 Lamont, Saanichton, B.C., Canada. 1960 (1960) [S.].
Beebe, Hiram E., 1847 N. Wilcox Ave., Hollywood 28, Calif. 1948.
Beecher, William J., Chicago Nat. Hist. Mus., 2001 N. Clark St., Chicago 14, Ill. 1948.
Beer, James R., Entomology & Econ. Zoology Dept., Univ. Minnesota, St. Paul 1, Minn. 1957.
Behle, William H., Biology Bldg., Univ. Utah, Salt Lake City 12, Utah. 1933 (1958) [L.].
Beidleman, R. G., Zoology Dept., Colorado College, Colorado Springs, Colo. 1948.
Belcher, Sir Charles F., Burnley House, Kokstad, Cape Province, South Africa. 1948.
Belcher, Paul E., 230 Mineola Ave., Akron 13, Ohio. 1945 (1950) [S.].
Belkin, Daniel A., 6255 Drexel Ave., Los Angeles 48, Calif. 1954.
Bell, A. Weir, Life Sciences Dept., L.A. City College, Los Angeles 29, Calif. 1936.
Bellrose, Frank C., 303 S. Broadway, Havana, Ill. 1953.
Belt, Charles B., 233 Broadway, New York 7, N.Y. 1956.
Belt, R. Elmer, 1893 Wilshire Blvd., Los Angeles 5, Calif. 1942.
Bendell, James F., Zoology Dept., Univ. British Columbia, Vancouver 8, B.C., Canada, 1957.
Bender, Richard O., Cobb's Mill Rd., R.D. 1, Bridgeton, N.J. 1951 (1956) [S.].
Benjamin, Gilbert G., Jr., 11554 McLennan Ave., Granada Hills, Calif. 1939.
Benson, C. W., Game & Tsetse Dept., Box 1, Chilanga, Northern Rhodesia, Central African Federation. 1959.
Benson, Seth B., 645 Coventry Rd., Berkeley 7, Calif. 1927.
Berger, Andrew J., Anatomy Dept., East Medical Bldg., Univ. Michigan, Ann Arbor, Mich. 1947.
Berger, Daniel D., 510 E. MacArthur Rd., Milwaukee 17, Wis. 1954.
Bergstrom, E. Alexander, 37 Old Brook Rd., West Hartford 7, Conn. 1942.
Berlioz, Jacques, Museum d'Histoire Naturelle, 55 Rue de Buffon, Paris Ve, France. 1959.
Berry, William D., 30 Rockridge Rd., Fairfax, Calif. 1951.
Bertoni, A. de Winkelreid, Puerto Bertoni, Paraguay. 1959.
Bialac, James T., 4706 N. 16th Dr., Apt. 4, Phoenix, Ariz. 1955.
Bibbee, Paul C., Concord College, Athens 4, W. Va. 1947.
Biddle, John A., 418 Westbourne St., La Jolla, Calif. 1947 (1949) [S.].
Billeb, Stephen L., 307 Vicente St., San Francisco 27, Calif. 1960.
Binford, Laurence C., Museum of Zoology, Louisiana State Univ., Baton Rouge 3, La. 1955.
Bird, Dick, 2721 Assiniboine Ave., Regina Saskatchewan, Canada. 1956.
Bishop, John W., 3260 Donley, San Diego 17, Calif. 1960.
Blackford, John L., Libby, Mont. 1952 (1952) [L.].
Blackstone, Robert E., 10363 Calvin Ave., Los Angeles 25, Calif. 1953.
Blake, Charles H., Box 613, Hillsboro, N.C. 1947.

Blake, Emmet R., Chicago Nat Hist. Museum, Roosevelt Rd. and Lake Shore Dr., Chicago 5, Ill. 1956.

Blanchard, Dean H., Box 989, Santa Barbara, Calif. 1937.

Bleitz, Don, 2047 Castilian Dr., Hollywood 28, Calif. 1944 (1951) [S.], (1952) [L.].

Boag, D. A., 11623 Saskatchewan Dr., Edmonton, Alberta, Canada. 1957.

Bock, Walter, Biological Labs., Harvard Univ., Cambridge 38, Mass. 1954.

Bohl, Wayne H., Wildlife Research, Bureau Sports Fisheries, Fish & Wildlife Service, U.S.D.I., Washington 25, D.C. 1953.

Bolander, Gordon L., 4411 Guerneville Rd., Santa Rosa, Calif. 1943.

Bond, Richard M., Virgin Islands Corp., Kingshill, St. Croix, U.S. Virgin Islands. 1936 (1949) [S.].

Bondi, Joseph, 355 Hutchinson Blvd., Mount Vernon, N.Y. 1960 (1960) [S.].

Bone, Fred W., 609 Yale Ave., Riverview Heights, New Brunswick, Canada. 1959.

Booth, Ernest S., Box 1326, Escondido, Calif. 1939.

Booth, Katherine F., 1085 Bank St., Painesville, Ohio. 1953.

Borell, Adrey E., Soil Conservation Service, Bldg. 50, Federal Center, Denver 25, Colo. 1918.

Borneman, John C., Edgemont Manor, Apt. 304, 1724 N. Edgemont St., Los Angeles 27, Calif. 1959 (1959) [S.].

Borrero, Jose I., Instituto de Ciencias Naturales, Universidad Nacional, Apdo. Nac. No. 2535, Bogota, Colombia. 1959.

Bosbyshell, F. H., 545 S. Figueroa St., Los Angeles 17, Calif. 1951 (1957) [S.].

Boschma, H., Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands. 1959.

Bossert, Elizabeth, 1780 Rotary Dr., Los Angeles 26, Calif. 1959.

Bourliere, F., 15 Avenue de Tourville, Paris 7, France. 1956.

Bourne, Raymond D., Box 187, Oxford, Ohio. 1947 (1951) [L.].

Bowdish, B. S., 16 Van Horn St., Demarest, N.J. 1910.

Bowen, Lydia S., 841 Earlham St., Pasadena 4, Calif. 1948.

Bowers, Darl E., Mills College, Oakland 13, Calif. 1949.

Bowers, J. Basil, 22275 Lantis Lane, Los Altos, Calif. 1947.

Bowman, Mabelle D., 51 Marr Ave., Oakland 11, Calif. 1949.

Bowman, Robert I., 1069 Sterling Ave., Berkeley 8, Calif. 1948.

Boyd, George H. St. Clair, R.R. 1, Maple Bay Rd., Duncan, Victoria Island, B.C., Canada. 1959.

Boyer, G. Paula, 420 E. Second St., Roselle, N.J. 1958.

Boyne, Elmer M., 624 Nixon Ave., Reno, Nev. 1951.

Bracelin, Mrs. H. P., 2214 Vine St., Berkeley 9, Calif. 1930.

Brackbill, Hervey G., 2620 Poplar Dr., Baltimore 7, Md. 1945 (1951) [S.].

Bradburn, Donald M., 440 Bellaire Dr., New Orleans 24, La. 1953 (1959) [S.].

Brandt, Jim, 109 11th St., Sparks, Nev. 1959.

Brandt, John H., Trust Territory of Pacific Islands, Truk, East Caroline Islands, via Guam. 1956.

Brattstrom, Bayard H., Biology Dept., Orange County State College, Fullerton, Calif. 1956.

Brauner, Joseph H., 3855 Potomac Ave., Los Angeles 8, Calif. 1946.

Breitenbach, Robert P., Zoology Dept., Univ. Missouri, Columbia, Mo. 1957.

Brem, George, Jr., 6 N. Miller Ave., Gilroy, Calif. 1958.

Briggs, Steve, 2700 Gordon Dr., Naples, Fla. 1960.

Brittan, Martin R., Life Sciences Dept., Sacramento State College, 6000 J St., Sacramento 19, Calif. 1948.

Broadbooks, Harold E., Southern Illinois Univ., Alton, Ill. 1942.

Brode, J. Stanley, 478 24th St., Santa Monica, Calif. 1934 (1960) [S.].

Brodkorb, Pierce, Biology Dept., Univ. Florida, Gainesville, Fla. 1940.

Brodrick, Neva M., 721 Cleveland Ave., Oakland 6, Calif. 1949.

Brody, Gerald L., University Hospital, Univ. Michigan, Ann Arbor, Mich. 1955.

Brooks, Matilda M., 630 Woodmont Ave., Berkeley 8, Calif. 1949 (1957) [S.].

Brown, Asa L., Janesville, Calif. 1938 (1951) [S.].

Brown, Ethel P., 4254 Ampudia St., San Diego 3, Calif. 1946.

Brown, Jerram L., Museum of Vertebrate Zoology, Berkeley 4, Calif. 1952.

Brown, Martin D., Jr., 9131 Canfield Dr., Whittier, Calif. 1954 (1960) [S.].

Brown, Ollie D., 8964 Wonderland Ave., Los Angeles 46, Calif. 1952.

Brown, Richard M., Crater Lake National Park, Fort Klamath, Ore. 1958.

Brown, Robert L., Carlyle, Mont. 1960.

Brown, William L., 173 Hillhurst Blvd., Toronto 12, Ontario, Canada. 1957.

Bruns, Herbert, Feldbrunnenstrasse 58, Vogelschutzwarte, Hamburg 13, Germany. 1950.

Bruns, James H., 1571 Henry Clay Ave., New Orleans 18, La. 1949.

Bryan, George A., Jr., Museum of Vertebrate Zoology, Berkeley 4, Calif. 1959.

Bryant, Charles E. W., 394–396 Collins St., Melbourne, Australia. 1959.
Bryant, Harold C., 245 Glorietta Blvd., Orinda, Calif. 1910 (1920) [L.].
Bryens, Oscar McK., Route 1, White Pigeon, Mich. 1927 (1960) [S.].
Buchanan, O. Marcus, Jr., Zoology Dept., Univ. California, Los Angeles 24, Calif. 1960.
Bull, Dan B., Box 608, La Mesa, Calif. 1950 (1951) [S.].
Burch, Mrs. John Q., 4206 Halldale Ave., Los Angeles 62, Calif. 1947.
Burgess, Anthony B., 3880 Blenheim St., Vancouver 8, B.C., Canada. 1959.
Burkhart, Harriet H., Rt. 3, Old Valley Road, Union City, Pa. 1958.
Burleigh, Thomas D., Fish & Wildlife Service, U.S. National Museum, Washington 25, D.C. 1956.
Burrell, Harry F., 5133 Vesper Ave., Sherman Oaks, Calif. 1960.
Bursewicz, John, Vivarium Bldg., Wright and Healey Sts., Champaign, Ill. 1958.
Burt, William H., Museum of Zoology, Univ. Michigan, Ann Arbor, Mich. 1928.
Burtis, Prentis T., 6035 Park Ave., Richmond, Calif. 1956.
Bushman, John B., Ecological Research, Univ. Utah, Dugway, Utah. 1952.
Buss, Irven O., 117 Science Bldg., Washington State Univ., Pullman, Wash. 1955.
Buzzell, Jerry, 51 Avalon Dr., Los Altos, Calif. 1959.

C

Cade, Tom J., Zoology Dept., Syracuse Univ., Syracuse 10, N.Y. 1950.
Cady, Walter G., 3350 Calvert Rd., Pasadena 8, Calif. 1951.
Cahalane, Victor H., 80 Fernbank Ave., Delmar, N.Y. 1938.
Calaby, J. H., Western Australian Museum, Beaufort St., Perth, Western Australia. 1955.
Calder, James A., 6851 Orangethorpe, Buena Park, Calif. 1917.
Calef, Robert T., Bay City Junior College, Bay City, Mich. 1955 (1959) [S.].
Camp, Charles L., Museum of Paleontology, Univ. California, Berkeley 4, Calif. 1909.
Campbell, Elizabeth W. C., Rt. 2, Box 871–A, Tucson, Ariz. 1940 (1949) [S.].
Campbell, Howard, 7500 Leah Dr., N.E., Albuquerque, N.M. 1959.
Campbell, John M., Dept. Sociology & Anthropology, George Washington Univ., Washington, D.C. 1957.
Campbell, Raymond A., Star Route, Jamul, Calif. 1953.
Cannon, Jerauld C., 872 W. Rillito Ave., Tucson, Ariz. 1957 (1959) [S.].
Cant, Gilbert, 716 Guion Dr., Mamaroneck, N.Y. 1960.
Cardiff, Bruce E., 633 W. Randall Ave., Rialto, Calif. 1948.
Cardiff, Eugene A., 2736 Court St., Rialto, Calif. 1947.
Cardon, Wayne, 13301½ San Antonio Dr., Norwalk, Calif. 1959.
Carey, Joshua H., R.R. 2, Boston State Rd., Hamburg, N.Y. 1936.
Carey, O. J., Game Control Officer, P. O. Mzuzu, Nyasaland, Central African Federation. 1959.
Carnes, Lucille H., 31 Dogwood Lane, Tenafly, N.J. 1947.
Carpenter, Eugene E., 48 W. Spartan City, South 7th Ave., San Jose 12, Calif. 1960.
Carter, E. W., 234 Muirfield Rd., Los Angeles, Calif. 1958 (1958) [S.].
Carter, Frances, 2200 College Ave., Berkeley 4, Calif. 1934.
Cassel, J. Frank, Zoology Dept., North Dakota Agr. College, Fargo, N.D. 1946.
Caswell, Herbert H., Jr., Eastern Michigan Univ., Ypsilanti, Mich. 1950.
Chalif, Edward L., 37 Barnsdale Rd., Short Hills, N.J. 1948 (1952) [L.].
Chamberlain, Samuel R., Box 593, Refugio, Texas. 1957 (1958) [L.].
Chambers, Carl W., 514 Marquette St., Pacific Palisades, Calif. 1936.
Chambers, W. Lee, R.R. 1, Box 410, Topanga, Calif. 1897 (1919) [L.], (1936) [Honorary].
Chaney, Hope B., 932 Tiverton Ave., Los Angeles 24, Calif. 1957.
Chaniot, George E., Jr., 320 E. Washington, Apt. 5, Ann Arbor, Mich. 1957.
Chapelle, Lt. Col. Francis O., M.S.C., 98th General Hospital, APO 34, New York, N.Y. 1954.
Chapin, James P., American Museum of Nat. Hist., Central Park West at 79th St., New York 24, N.Y. 1959.
Chappell, Edward M., Box 1085, Escondido, Calif. 1958.
Childs, Henry E., Jr., Cerritos College, Norwalk, Calif. 1947.
Chinery, D. J., 119 Kingsmead Ave., Worcester Park, Surrey, England. 1959 (1960) [S.].
Chisholm, Alexander H., Angus & Robertson, Ltd., 89 Castlereagh St., Sydney, Australia. 1959.
Chisholm, Bonnie R., Fall City, Wash. 1960.
Christensen, Frank, 8045 Emerson Ave., Los Angeles 45, Calif. 1957.
Christensen, Ruth, 8045 Emerson Ave., Los Angeles 45, Calif. 1953.
Christman, Gene M., Museum of Vertebrate Zoology, Berkeley 4, Calif. 1946.
Church, Ronald L., 6 Ivy Dr., Orinda, Calif. 1954.
Clapp, Clara M., 3962 Dalton Ave., Los Angeles 62, Calif. 1956.

Clark, Ervil D., 250 Cold Springs Rd., Angwin, Calif. 1957.
Clark, George A., Jr., Peabody Museum, Yale Univ., New Haven, Conn. 1956.
Clarke, Oscar F., 1012 Indianapolis Ave., Riverside, Calif. 1951.
Clarke, William S., Jr., Box 167, State College, Pa. 1948 (1949) [S.].
Clarkson, Mrs. Erwin O., Wing Haven, 248 Ridgewood Ave., Charlotte, N.C. 1945 (1953) [L.].
Clary, Marjorie D., 7630 Cimarron St., Los Angeles 47, Calif. 1929.
Clattenburg, Albert E., Jr., 4764 33rd St. North, Arlington 7, Va. 1947.
Clay, C. Irvin, Box 353, Eureka, Calif. 1910 (1923) [L.].
Clements, H. Everest, 64 Merriman St., Rochester 7, N.Y. 1951 (1951) [L.].
Clements, William F., 316 Bronwood Ave., Los Angeles 49, Calif. 1960.
Clow, Marion, 128 Moffett Rd., Lake Forest, Ill. 1945.
Clyde, Dale P., 201 Laurel St., San Francisco 18, Calif. 1957.
Coffey, Ben B., Jr., 907 Union Planters Bldg., Memphis 3, Tenn. 1957.
Coggeshall, Robert D., Billington Rd., East Aurora, N.Y. 1956.
Coggins, Herbert L., 2764 Filbert St., San Francisco 9, Calif. 1910.
Cogswell, Howard L., Biological Sciences Dept., Mills College, Oakland 13, Calif. 1940.
Cole, Helen M., 1746 Sulgrave Rd., Louisville 5, Ky. 1956.
Collias, Nicholas E., Zoology Dept., Univ. California, Los Angeles 24, Calif. 1958.
Collier, Gerald, Zoology Dept., Univ. California, Los Angeles 24, Calif. 1953.
Collins, Henry H., Jr., 1200 Post Rd., Scarsdale, N.Y. 1960.
Colton, Harold S., Museum of Northern Arizona, Box 601, Flagstaff, Ariz. 1936.
Colvin, Lily, 11937 Goshen Ave., Los Angeles 49, Calif. 1957.
Combellack, Rose, 3021 Friendly St., Eugene, Ore. 1952.
Compton, Lawrence V., Biology Div., Soil Conservation Service, Washington 25, D.C. 1927.
Cone, Clarence D., Jr., 29 Reynolds Dr., Hampton, Va. 1959.
Cone, Lt. Col. Hutchinson I., Jr., Box 553, Richmond, Ky. 1940.
Connon, Herold, 288 Lester Ave., Oakland 6, Calif. 1958.
Constable, Robert S., Zoology Dept., Univ. California, Los Angeles 24, Calif. 1958.
Conway, William G., N.Y. Zoological Park, Bronx 60, N.Y. 1960 (1960) [S.].
Cook, Waldo S., Rt. 1, Box 183–A, Ukiah, Calif. 1959 (1959) [S.].
Cooper, Ruth B., D–43, U.S.N.A.B., Little Creek, Va. 1944.
Cope, James B., Earlham College, Richmond, Ind. 1957.
Coppa, Jon B., Box 935, Kingman, Ariz. 1960.
Coppersmith, Michael M., Camp O–Ongo School, Sky Forest, Calif. 1960.
Cottam, Clarence, Welder Wildlife Foundation, Box 1396, Sinton, Texas. 1926 (1958) [S.].
Cottrell, George W., Jr., Harvard College Library, Cambridge 38, Mass. 1945.
Couffer, Jack C., 705 Poppy Ave., Corona del Mar, Calif. 1942.
Covel, Paul F., 2860 Delaware St., Oakland 2, Calif. 1935.
Cowan, Ian McT., Zoology Dept., Univ. British Columbia, Vancouver, B.C., Canada. 1937.
Cowles, Raymond B., Zoology Dept., Univ. California, Los Angeles 24, Calif. 1928.
Craig, Alan M., Disbursing Office, U.S. Naval Air Sta., Glynco, Brunswich, Ga. 1954.
Craig, Ethel B., 1763 Royal Oaks Dr., Apt. A-19, Duarte, Calif. 1956.
Craig, James L., 29 Mayfair Ave., Springfield 4, Mass. 1960 (1960) [S.].
Cramer, Frances L., 921 W. 36th Pl., Los Angeles 7, Calif. 1940 (1943) [L.].
Crawford, Franklin G., 3279 Rubio Canyon Rd., Altadena, Calif. 1939.
Crippen, Robert G., Museum of Vertebrate Zoology, Berkeley 4, Calif. 1958.
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